Palæontographica Americana

Begun in 1916

NUMBER 58 **AUGUST 24, 1994**

Fruits and Seeds of the Middle Eocene Nut Beds Flora, Clarno Formation, Oregon

by

Steven R. Manchester

Paleontological Research Institution
1259 Trumansburg Road
Ithaca, New York, 14850 U.S.A.

ISSN 0078-8546
ISBN 0-87710-435-2
Library of Congress Card Number: 94-65491

Printed in the United States of America
Allen Press, Inc.
Lawrence, KS 66044, U.S.A.

CONTENTS

Conifers

Angiosperms

LIST OF ILLUSTRATIONS

LIST OF TABLES

FRUITS AND SEEDS OF THE MIDDLE EOCENE NUT BEDS FLORA, CLARNO FORMATION, OREGON

Steven R. Manchester

Florida Museum of Natural History
University of Florida
Gainesville, FL 32611

ABSTRACT

Permineralized fruits and seeds from the Nut Beds flora of the Clarno Formation, north-central Oregon, are described and illustrated, providing the first comprehensive treatment of a North American fossil fruit and seed assemblage and facilitating comparison with European Tertiary fruit and seed assemblages. Newly obtained radiometric dates, along with vertebrate correlations, indicate a Middle Eocene age of about 44 million years for the assemblage. Based upon examination of approximately 20,000 specimens, 145 genera and 173 species are recognized, providing much new data for systematic, evolutionary, biogeographic and paleoecologic interpretation. Seventy-five genera and 102 species have been identified to 35 living families; 70 genera and 71 species represent form genera of unknown familial affinity and may belong both to extinct genera and to extant genera whose affinities may come to light with future work.

Among the 102 species attributed to extant families, 58% belong to extant genera, 30% are extinct genera, and 22% are stereotype genera (identical in the characters preserved to more than one modern genus). Trees and lianas are well represented, nearly to the exclusion of herbs. The only herbaceous angiosperm identified is *Ensete* (Musaceae). The proportion of the identified taxa that represent lianas or climbers is high (43% of the 69 species for which growth form may be inferred) including 14 species of Menispermaceae, seven of Icacinaceae and six of Vitaceae. The disseminules range in size from about 0.5 mm to 85 mm; about 15 are winged and suitable for wind-dispersal, but most are medium to large in size and represent drupes and berries adaptive for biotic dispersal.

Among the extant genera determined, some are exclusively temperate in distribution today (e.g., *Taxus*, *Emmenopterys*, *Parthenocissus*), while others are exclusively paratropical to tropical (e.g., *Ensete*, *Mastixia*, *Iodes*, *Ampelocissus*, and, among the vertebrate fossils, a crocodilian). Many of the genera are distributed today in both temperate and tropical areas. Despite the occurrence of many taxa that are temperate today, the presence of Musaceae, Palmae and other taxa that typically are frost-intolerant today, combined with the high diversity of lianas, is taken as an indication that the climate was comparable to that which supports paratropical rainforest vegetation today. The flora shares 24% of its genera with the Early to Middle Eocene flora of western Europe, indicating that one or more land connections were viable during or prior to the Middle Eocene. Among extant genera represented in the Nut Beds assemblage, the greatest similarity is with the extant flora of eastern Asia. The identified families are, among the conifers: Taxaceae (3 genera), Pinaceae; among the angiosperms: Actinidiaceae, Alangiaceae, Anacardiaceae (2 genera), Annonaceae, Araliaceae, Betulaceae (2 genera), Cornaceae (6 genera), Fagaceae (2 genera), Flacourtiaceae, Hamamelidaceae, Hydrangeaceae, Icacinaceae, Juglandaceae (4 genera), Lauraceae (3 or more genera), Leguminosae, Lythraceae, Magnoliaceae, Menispermaceae, (13 genera), Musaceae, Palmae, Platanaceae (3 genera), Rosaceae, Rubiaceae, Sabiaceae (2 genera), Sapindaceae (2 genera), Sapotaceae, Schisandraceae, Staphyleaceae, Symplocaceae, Theaceae, Ulmaceae (4 genera), and Vitaceae (4 genera).

ACKNOWLEDGEMENTS

This work is dedicated to the memory of Thomas J. Bones (Text-fig. 1), who collected the majority of specimens upon which this investigation is based and whose enthusiasm helped to kindle my own interest in paleobotany as a high school student. Many others assisted me in collecting at the locality as participants in paleobotanical programs sponsored by the Oregon Museum of Science and Industry during the summers of 1972 to 1989, including Alexander Atkins, Scott Blanchard, Kris Goertz, Ian Gordon, C. Bruce Hanson, Carol Hardman, Elizabeth Harding, Kathy Harvey, Joyce Lenz, Maureen Muldoon, Duane Olson, Jerome McFadden, Ellen Pasternack, John Ries, Josephine Spitzer, Michele Vowell, Eric and Mike Weinstein and others. I thank former and present staff of the Oregon Museum of Science and Industry, including John M. Armentrout, Bruce Hansen, Michael C. Houck, and Joseph Jones, III, and members of the Oregon Agate and Mineral Society, including Gar Hurley, William and Gertrude Hall, for their support of student field programs in Clarno paleobotany.

Special thanks are due to Carrie L. Roose, for invaluable help in sorting, measuring and cataloguing specimens, assistance with initial taxonomic analyses and in preparing the geologic map and preliminary diagrams. C. Bruce Hanson provided help in interpreting the local geology. Wendy Zomlefer assisted with preparation of the text-figure illustrations. David Dilcher provided access to equipment and facilities as well as helpful encouragement throughout this research. N. Gary Lane kindly provided access to a Microslice II annular diamond saw for sectioning the seeds.

Text-figure 1.—Thomas J. Bones, photographed in 1977 at an excavation on the top of Face 3. Mr. Bones collected here for about 40 years, and provided the massive collections upon which much of this monograph is based.

Advice in the preparation of latex and silicone casts was given by William Simpson and Russell McCarty. Help with identifications was provided by Margaret Collinson, Robert Kaul, Peter Endress, Paul Grote, Dieter Mai, Charles N. Miller, Richard A. Scott, and Bruce H. Tiffney. Grammatical advice on the construction of new Latin binomials was provided by Benoit LePage and Christine Kampny.

Access to paleobotanical collections was provided by Scott Wing, Francis Hueber, and James P. Ferrigno (U.S. National Museum, Washington, D.C.); Howard E. Schorn (Museum of Paleontology, University of California, Berkeley), Wesley Wehr (Burke Memorial Washington State Museum, University of Washington, Seattle), Charles Beck and Robyn Burnham (Museum of Paleontology, University of Michigan), Andrew Knoll (Harvard University), Leo Hickey (Peabody Museum of Natural History, Yale University, New Haven), Chris Hill and Cedric Shute (Natural History Museum, London, England), Christiane Blanc (Muséum National d'Histoire Naturelle, Paris, France), Friedemann Schaarschmidt (Senckenberg Museum, Frankfurt, Germany). Access to extant fruit and seed collections was provided by Charles Gunn (National Seed Herbarium), Peter Stevens (Harvard University Herbaria), Norris Williams and Kent Perkins (University of Florida Herbarium). Helpful comments on the manuscript were provided by David Dilcher and Herbert Meyer. I also want to thank the reviewers, Bruce H. Tiffney and Else Marie Friis, for invaluable comments and suggestions.

This research was supported in part by the following National Science Foundation grants: DEB 81-11-89, EAR 8707523, EAR 8904234, BSR 9007495, EAR 9322765. This publication represents work that was initiated with the facilities and support of Indiana University and completed at the University of Florida. Publication costs were met in part by funds from the Gatorade Account of the University of Florida. This publication is number 410 in the University of Florida Contributions to Paleobiology.

INTRODUCTION

A diverse assemblage of well-preserved Middle Eocene plant remains occurs in the type area of the Clarno Formation about 3 km east of the community of Clarno, north-central Oregon, in a locality known as the Nut Beds. The site yields abundant fossil woods (Scott and Wheeler, 1982), leaves (Manchester, 1981), and exquisitely preserved fruits and seeds (Scott, 1954; Bones, 1979). Because fossil fruit and seed floras are relatively rare in North America, the Clarno Nut Beds flora provides an important link for paleobotanical comparisons with the Tertiary of Europe, where fruit and seed assemblages are abundant and relatively well studied. The Clarno flora often has been cited in phytogeographic discussions because taxonomic similarity with European fruit and seed floras provides evidence of broad floral continuity between Europe and North America during the Eocene (Scott, 1954; Chandler, 1964; Wolfe, 1972, 1975; Tiffney, 1985a, 1985b; Collinson, 1988; Manchester, 1988). Only a small portion of the Clarno flora has been described, however, and the actual extent of generic and specific similarity between the Eocene floras of North America and Europe has not been well documented.

The paleobotanical and phytogeographic significance of the Clarno flora was first shown by Scott (1954) in a monograph detailing the morphology and relationships of ten species from the Nut Beds locality. Scott's work demonstrated the presence of genera with Old World tropical affinities in the Eocene of western North America, and documented several genera in common with the Eocene London Clay flora of England. He also called attention to the presence of both extant and extinct genera, a finding somewhat at odds with Tertiary leaf studies of the time. Subsequently, an expanded taxonomic list of Clarno fruits and seeds was published (Scott, in Chandler, 1964, p. 58) including 32 additional genera from the locality. Until now, these additional taxa have not been formally described. Bones (1979) published an atlas depicting some of the diversity present in the Nut Beds fruit and seed assemblage, including a variety of new but undescribed species. Several additional fruit and seed taxa from the Nut Beds have been treated in separate accounts (Manchester, 1986, 1987a, 1987b, 1988, 1989a; Manchester and Kress, 1993), but a comprehensive treatment of the flora has not been attempted previously. The Nut Beds fossils represent one of the warmest climatic intervals in the Tertiary of North America, a time when thermophilic vegetation was spread well into the northern latitudes (Wolfe and Poore, 1982; Wolfe, 1985).

Because of the excellent details of morphology and anatomy preserved in silicified fruits and seeds from the Nut Beds flora, specimens from this assemblage provide the rare opportunity to investigate the internal structure of Eocene plant reproductive organs. Such specimens enable a well-informed assessment of taxonomic affinities, and make it possible to test whether affinities inferred from external morphology are upheld by internal anatomy. The Nut Beds specimens thus provide insight into the structure and affinities of various extinct and extant genera of fruits and seeds that are known only from molds or impressions at other fossil localities.

This monograph is an attempt to provide a thorough taxonomic treatment of all known fruit and seed species from the Nut Beds flora, including taxa of undetermined familial affinity as well as those which can be identified confidently to modern families and genera. The resulting data base: 1) provides new systematic data on plants present during the Middle Eocene in western North America; 2) contributes information on the evolutionary status of various gymnosperm and angiosperm taxa in the Middle Eocene of the northern hemisphere; 3) provides insight into the environment and climate under which the Nut Beds vertebrate fauna existed; 4) enables comparison with other Eocene fossil floras of the northern hemisphere and to modern floristic regions to gain some understanding of timing and routes of phytogeographic exchange.

GEOGRAPHIC AND GEOLOGIC SETTING

The Clarno Formation is a terrestrial sequence of andesitic to basaltic lavas and intrusives, ash flows, volcanic mudflows, and tuffaceous sediments exposed along the Blue Mountain Anticline in north-central Oregon. The distribution, stratigraphy, age, structure, composition and source vents of the formation are reviewed by Walker and Robinson (1990). Petrologic and trace element studies suggest that the volcanism may have been in response to subduction zone magmatism (Rogers and Novistsky-Evans, 1977; Noblett, 1981). The formation is well known for its paleontologic importance and is the focus of the Clarno Unit of John Day Fossil Beds National Monument. Leaf impressions and silicified wood occur in tuffaceous strata in many areas of the Clarno Formation (Hergert, 1961; Manchester, 1986, 1991). Fruits and seeds, which occasionally occur in the same strata as leaves, are usually preserved as impressions or compressions. However, the Nut Beds locality is unusual because it provides uncompressed, three-dimensionally preserved, permineralized, fruits and seeds.

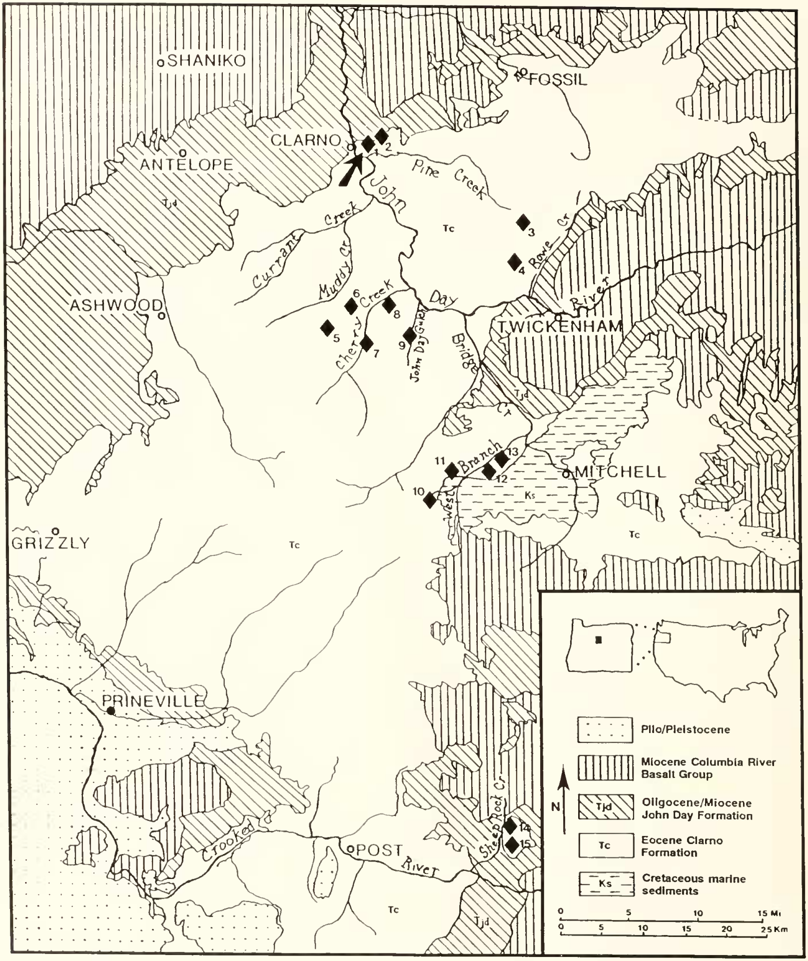
The Nut Beds locality (UF loc. 225) is situated in the type area of the Clarno Formation, at 44°56′36″ N lat., 120°25′34″ W long. (SW ¼, SE ¼, sec. 27, T 7 S, R 19 E), Wheeler County, Oregon (Text-fig. 2). It is a resistant, buff-colored, cliff-forming unit about 10 meters thick, exposed over an area of about one hectare along the western side of Hancock Canyon (Text-fig. 3). The term "nut beds" was first applied by amateur fossil collectors in the 1940's because of the abundance of petrified walnuts and other fruits and seeds found there. Fossil plants occur throughout the vertical and horizontal extent of the exposure. The same locality is also significant for its vertebrate fauna, which constitutes the only known Middle Eocene terrestrial mammalian fauna in the Pacific Northwest (Stirton, 1944; Hanson, 1973, p. 56 in Retallack, 1991).

The complex geology of the local area surrounding the Middle Eocene Nut Beds locality, and stratigraphic relations with the Late Eocene/Early Oligocene Hancock Quarry vertebrate locality 1 km to the north (Text-fig. 3), are currently under investigation (C. B. Hanson, pers. comm.; G. Retallack, pers. comm.). Hanson (pers. comm., 1992) distinguishes five unconformity-bounded units in the type area of the Clarno Formation. The Nut Beds deposit occurs low in the section, within the second unit, and predates an adjacent andesitic plug[1] which was a source for clasts found in subsequently deposited sediments of the Clarno Formation in its type area. The Hancock Quarry fauna (Mellet, 1969; Hanson, 1973, 1991) and flora (McKee, 1970) locality is situated in Hanson's uppermost unit, an upper Clarno valley-fill deposit containing clasts from the andesitic plug. Retallack (pers. comm., 1993), however, reports finding clasts of the andesitic plug[1] in the Nut Beds sediment and considers the Nut Beds to correlate with the upper part of a sequence of lahars and tuffs exposed 1 to 2 km north and east in Hancock Canyon.

The Nut Beds deposit is composed of tuffaceous silt-

---

[1] New information available; see Notes added in proof, p. 200.



Text-figure 2.—Geologic map and index map (inset) of the John Day and Crooked River Basins, north-central Oregon, showing location of the Nut Beds (arrow) and other paleobotanical localities of the Clarno Formation. Localities: 1. Nut Beds, 2. Hancock Quarry, 3. Dry Hollow, 4. Left Hand Canyon, 5. Horseheaven, 6. White Cliffs, 7. Indian Rocks (classic Cherry Creek site), 8. Red Gap, 9. John Day Gulch, 10. Ochocco Summit, 11. Doolittle Flat, 12. Alex Canyon, 13. Classic West Branch Creek locality, 14. Brummers Spring, 15. Sheep Rock Creek (Teater Road site). Geologic map adapted from Walker (1977).

Text-figure 3.—Oblique, northward, aerial view overlooking the Middle Eocene Nut Beds locality, with exposure faces labeled 1 to 5. The dark unvegetated strata overlying the Nut Beds are a sequence of paleosols locally called Red Hill (RH) that is capped by the basal ignimbrite of the John Day Formation. Other localities in the distance include the Upper Eocene Hancock Quarry (HQ) in the upper part of the Clarno Formation and the Oligocene Dugout Gulch leaf locality (DG) in the lower part of the John Day Formation. Iron Mountain, capped by Miocene Columbia River Basalts, forms the horizon.

stones, sandstones and conglomerates thoroughly cemented by silica and calcium carbonate. The stratigraphic column at the Nut Beds is about ten meters thick, consisting of a lower half with alternating beds of siltstone and sandstone mostly 0.1–0.6 m in thickness, and an upper half with thicker beds of alternating siltstone, sandstone and andesitic conglomerate (Text-fig. 4). Clasts of the conglomerate are subangular to rounded, generally less than 4 cm in diameter, and are matrix-supported. Permineralized wood, fruits and seeds occur throughout the vertical section, in siltstone, sandstone and conglomerate layers, with the greatest concentrations being in the uppermost strata. The vertebrate fossils are confined to the middle and upper strata, often in conglomerate, and are usually preserved as disarticulated bones. Impressions of leaves occur at various levels within the deposit, but are most abundant and well-preserved in siltstones near the base of the section (Manchester, 1981).

Abundant *Equisetum* stems and occasional fern rhizomes are found in growth position in some of the siltstone layers. In some parts of the deposit *Equisetum* stems may be traced vertically through 0.7 m of sediment (Retallack, 1981), indicating relatively rapid sediment accumulation (Scott, 1954) and shallow-water conditions. Predepositional abrasion is evident in some of the fossils (particularly fossil woods in the upper part of the section) and suggests that the assemblage includes transported as well as locally derived plant debris. Although well-preserved silicified wood is common, most pieces are small, predepositionally worn fragments; no standing stumps were confirmed.

The Nut Beds deposit is dissected by slumps and erosion into five outcrop faces, which, for reference, have been designated from south to north as Faces 1–5 (Text-fig. 3). Most of the vertebrate remains were recovered from the middle and upper portions of Faces 1 and 3. The fossil fruits and seeds described by Scott

Text-figure 4.—Profile view of the stratigraphic section at Face 3, showing alternation of beds (siltstone and sandstone/conglomerate). The lowest exposed layers contain leaves as well as some of the fruits. The most productive horizon for silicified wood and fruits was found to be in the massive upper layers.

(1954) and the *Hyrachyus* tooth described by Stirton (1944) were obtained from two beds situated in the gully between Faces 2 and 3. Thomas Bones collected fruits and seeds throughout the deposit, but found the richest horizons in excavations at the top of Face 3 (Text-fig. 1). Beds forming the uppermost meter of section on Face 3 contain an abundance of palm petiolar debris, abraded wood fragments, and small rounded fossiliferous chert clasts. The chert clasts, mostly 0.5–1.2 cm in diameter, may represent fragments of peat that were ripped up and carried along with the other clasts, or could alternatively represent small coprolites (C. B. Hanson, pers. comm.). Leaf remains in this upper horizon are usually folded or rolled, not flat-lying, and apparently were deposited during turbulent, rather than quiet-water conditions.

The sedimentary environment represented by the Nut Beds deposit has been interpreted as that of a lake delta deposit (Scott, 1954; C. B. Hanson, pers. comm.). This interpretation would account for the large amount of jumbled biotic debris, and the general thinning of the beds toward the northeast (C. B. Hanson, pers. comm.). However, typical lacustrine sediments, with fissile shales containing fish remains, as observed at other Clarno paleobotanical localities (e.g.. West Branch Creek, White Cliffs; Manchester, 1990), are not present at the Nut Beds. The lower portion of the section, with alternating siltstones and sandstones, might represent periodic flood deposition, whereas some of the thick, poorly sorted upper layers evidently represent a rapidly deposited slurry, possibly from the toe of a volcanic mudflow. Local hot springs may have been present, contributing toward rapid mineralization of biotic debris.

AGE

The value of the Nut Beds flora for biostratigraphic and paleobiogeographic correlations is enhanced by an accurate determination of its age. In previous paleobotanical assessments, age interpretations for the Clarno Nut Beds have ranged from "older than Upper Eocene" (Scott, 1954) to Early Oligocene (Wolfe, 1971, 1981). Although Wolfe (1981) attributed the Nut Beds ("late Clarno") flora to his Kummerian floral stage, of inferred Late Eocene/Early Oligocene age, his zonation is based on leaf species from a type section in the Puget Group of northwestern Washington (Wolfe, 1968). It is impossible to determine which of the Clarno fruit and seed species might correspond to the leaf species that Wolfe used to characterize his stages, and preliminary investigations of the Nut Beds leaf assemblage (Manchester, 1981) indicate that the flora is no more similar taxonomically to the Kummerian stage than to the older Franklinian and Ravenian stages. In any case, to eliminate potential for circularity, the age of the Nut Beds flora is best determined by means independent of paleobotanical correlation.

Radiometric dates reported for various parts of the Clarno Formation range from about 54 to 34 million years (Fiebelkorn et al., 1983), although the younger dates are questionable because the basal ignimbrite of the overlying John Day Formation has been dated at about 37 (Swanson and Robinson, 1968; Fiebelkorn et al., 1983; Vance, 1988) to 39.7 (Bestland et al., 1993) million years. The Clarno Formation represents a complex volcanic terrain characterized by abrupt lateral and vertical variation complicated by erosion, faulting and slumping. Therefore, it is difficult to trace individual units beyond local areas, and, as a result, the stratigraphic position of the Nut Beds in relation to other datable units of the Clarno Formation is not immediately obvious. Fortunately, the Nut Beds deposit itself contains a vertebrate fauna that can be correlated with North American land mammal stages, as well as volcanic clasts suitable for radiometric dating.

Stirton (1944) described a tooth of *Hyrachyus* from the Nut Beds, and on this basis clearly established an Eocene age for the locality. More complete cranial specimens of *Hyrachyus*, along with remains of five other mammalian vertebrates, including *Orohippus*, *Patriofelis* and *Telmatherium*, have been investigated by Hanson (1973) and clearly represent a Bridgerian fauna (Hanson, pers. comm., 1988). This fauna occurs within the Nut Beds along with the fruits and seeds, and should not be confused (cf., Wolfe, 1981, p. 44) with the younger Clarno fauna from Hancock Quarry, 1 km northeast of the Nut Beds, that is of Chadronian or Duchesnian age (Mellet, 1969; Hanson, 1973, pers. comm., 1988). By correlation with radiometrically dated faunas of the Rocky Mountain region, the Bridgerian vertebrate fauna of the Nut Beds indicates a Middle Eocene age of about 45 m.y.

Although a potassium-argon date of 34 million years was published for the Nut Beds (Evernden et al., 1964), such a young age (Late Eocene or Early Oligocene) is very doubtful because the basal ignimbrite of the overlying John Day Formation (situated about 30 meters stratigraphically above the Nut Beds) yields radiometric dates of about 37 (potassium-argon, Swanson and Robinson, 1968; fission track, Vance, 1988) to 39.7 (argon-argon, Bestland et al., 1993) million years. More recently, Vance (1988) obtained fission track dates of 43.6 and 43.7 (± 10%) m.y. based upon zircon extracted from Nut Beds sediment. In 1987, C. B. Hanson, B. D. Turrin and I collected a sample of water-reworked tuff with intact pumice clasts from a plant and bone-bearing stratum at the middle stratigraphic level of Face 1 in the Nut Beds. Ten plagioclase crystals isolated from this sample were analyzed by the single crystal laser fusion argon 40/39 technique and yielded dates ranging from 36.38 ± 1.31 to 46.8 ± 3.36 m.y. (B. D. Turrin, pers. comm., 1988). Statistically, these dates give an arithmetic mean of 42.98 ± 3.48 with a standard error of the mean, ± 1.10, and a weighted average of 43.76 ± 0.29 m.y., strikingly close to the fission track results of Vance (1988). Based upon the recently obtained radiometric ages and the vertebrate correlations, the age of the Nut Beds flora may be considered to be Middle Eocene, within the range of 43 to 45 million years old.

OTHER CLARNO FLORAS

Although this report is intended to be as comprehensive as possible for the fruit and seed assemblage of the Nut Beds locality, it should not be regarded as an exhaustive treatment of the Clarno flora. The Clarno Formation occurs over an area of about 4000 km^2 (Walker and Robinson, 1990) and includes many fossil plant localities (Text-fig. 2). The location and general character of some of these localities are reviewed by Hergert (1961) and Manchester (1990). Geographic coordinates for localities from which large collections have been made have been published previously (Manchester, 1986, p. 224; 1991, p. 717). Some of these sites, particularly the lacustrine deposits in the West Branch Creek and Cherry Creek drainages, include many species of leaves and compressed fruits that are not known from the Nut Beds. I have made reference to these other localities where appropriate in discussing the distribution of individual species.

Another occurrence of fossil fruits and seeds in the Clarno Formation is the Late Eocene (Duchesnean) Hancock Quarry vertebrate locality, situated 1 km northeast of the Nut Beds. This locality (UF 70) has provided abundant fruit and seed remains preserved as partially compressed carbonaceous casts and molds in claystone (McKee, 1970). Although anatomical details are not preserved, external morphology enables identification through comparison with the better preserved Nut Beds specimens. More than 500 specimens were collected from this site (collections at OMSI and UF) and is possible to distinguish about 30 taxa. Several genera are shared with the Nut Beds, including *Ampelocissus*, *Diploclisia*, *Juglans*, *Odontocaryoidea*, *Palaeophytocrene*, and *Vitis*. In addition to the genera recognized by McKee, I have observed specimens of *Alangium*, *Eohypserpa*, *Iodes*, *Iodicarpa*, *Mastixioidiocarpum* and *Pentoperculum* in the Hancock Quarry assemblage. Thus, it is clear that some of the Nut Beds genera persisted in the same region at least until the Late Eocene. There are, however, marked floristic differences between both of these assemblages and the Lower Oligocene Bridge Creek flora of the overlying John Day Formation (Chaney, 1927; Manchester and Meyer, 1987; Manchester, 1990).

The Brummers Spring locality (UF 254), also in the Clarno Formation, is located about 90 km south of the Nut Beds locality and 20 km east of Post, Oregon (Text-fig. 2). This locality has produced a small assemblage of silicified fruits and seeds including *Juglans*, *Magnolia*, *Mastixicarpum*, *Quercus*, and *Sabal*.

MODES OF PRESERVATION

Fossil fruits and seeds in the Nut Beds are preserved in various modes, ranging from compressions and impressions to molds and casts, to permineralizations. These different types of preservation, as applied to fossil plant tissues, are reviewed by Scott and Collinson (1983, p. 118). Compressed fruits and seeds, preserved along with leaf impressions near the base of the section (Manchester, 1981), usually lack internal structural details, but are useful in providing characters of wing morphology and venation. Three-dimensionally preserved specimens, including casts, molds and permineralizations, occur throughout the deposit.

Casts and molds lacking internal anatomy are common (Scott, 1954), but sometimes the internal tissues are preserved through permineralization by chalcedony and/or calcite. A single specimen may include more than one mode of preservation; for example, a cast of the locule may occur within the carbonized or permineralized remains of an endocarp. Permineralized seed remains are sometimes encountered within the locule cast.

Silicification appears to have been primary, and calcification secondary, as in the case of walnuts that are sometimes preserved with the locule filled by chalcedony and the nutshell infiltrated by calcite. The quality of preservation in permineralized specimens is variable, depending on porosity and durability of the tissues involved. Fleshy or pulpy outer fruit layers are rarely if ever preserved. Woody layers tend to be well-preserved, sometimes with excellent cellular detail. However, thin, hard, evidently impermeable layers typically are represented only as an airspace between the chalcedony internal mold and the siltstone outer mold of the structure, as in the case of seeds of *Annonaspermum*, *Fortunearites*, and *Bumelia*.

MATERIALS AND METHODS

Approximately 20,000 specimens were examined for this study. The majority of specimens were collected between 1942 and 1983 through the extraordinary efforts of Thomas J. Bones. Additional specimens were collected in the 1940's and 50's by A. W. Hancock, R. A. Scott, and, during the summers of 1974–1989, by S. R. Manchester with the help of many high school students (acknowledged p. 7) in conjunction with paleobotanical programs at Hancock Field Station, a natural science facility operated by the Oregon Museum of Science and Industry 1.5 km southeast of the Nut Beds.

The fossil disseminules range from less than 1 mm to 85 mm in length. Because the sediment is silica-cemented, standard washing and sieving techniques (Tiffney, 1990) are not effective in recovering specimens. Instead, the fossils are obtained through a labor-intensive process of prying out blocks of sediment and breaking the rock with hammers. Fruits and seeds are exposed in the matrix when intercepted by the resulting fracture planes. The percussion frequently causes the fruit or seed to pop out of the matrix. Sometimes outer layers of the fossil remain attached to the matrix mold. It is thus important to retain the associated mold for study as well as the more attractive cast. Thomas Bones collected large numbers of small seeds by crushing the matrix and sorting with the aid of a magnifying lens.

Because the type and quality of preservation varies greatly, even among specimens of the same species, it was necessary to sort the specimens under a dissecting microscope to recover the most informative samples for describing each species. Silica casts and molds replacing various tissues of the fruit or seed were useful for morphology and dimensions. Permineralized specimens were most valuable in providing the best details of internal morphology and anatomy. Permineralizations were not available for all species, but in many instances a careful examination of numerous specimens resulted in the recovery of at least a few permineralized examples that could be fractured or sawn to reveal internal morphology and anatomy. Compression and impression specimens were also found to be useful because they enable direct comparison with specimens from other Clarno localities where permineralizations are not available, and because they provide details of wing morphology and venation for samaras that usually are not evident in the permineralized specimens.

Morphology and anatomy was recorded photographically with Kodak Technical Pan 2415 film processed for medium contrast. Lighting for reflected light photography was provided from the upper left and lower right side of each specimen with a pair of small, diffuse tungsten lamps that could be oriented at various angles to provide optimal illumination of surface detail. Specimens of medium to large size (>8 mm diam.) were photographed with a Nikon FE camera with 100 mm Micronikkor lens. Macrography of smaller specimens (0.5–8 mm) was conducted with the FE camera mounted on a Nikon SMZ10 zoom stereo scope. Stereo-pair photographs were prepared of specimens which were subsequently fractured or serially sectioned. For stereo-pairs, successive pictures were taken with the specimen rotated 6 degrees on a teetering stand, or by using the stereo-photo option on the Nikon SMZ10 macroscope. The translucency and differential coloration of silicified specimens initially presented problems, obscuring surface details in photography. These problems were overcome by coating the specimens with palladium using a sputter coater prior to light micrography. The palladium was subsequently removed by soaking for 30 minutes in a saturated solution of sodium cyanide in water (Sela and Boyd, 1977). Small seeds, and minute surface details of larger specimens, were studied by standard techniques of scanning electron microscopy (SEM), using the Cambridge Stereoscan 250 and Hitachi S-450 SEM models.

Internal morphology and anatomy were revealed in some instances by studying fractured specimens with light and SEM microscopy and in other cases by serial sectioning. Specimens 1.5 mm to 25 mm in diameter were sectioned with a Microslice II annular diamond saw, with a very thin blade (0.05 mm thick) to minimize wastage (kerf loss about 0.15 mm) in the cutting process. Resulting wafers were photographed unetched in xylene, or dry after etching with hydrofluoric acid, by reflected light microscopy using a Wild M400 photomacroscope. For finer anatomical details the wafers were then used to make peels and/or ground thin sections for transmitted light microscopy. Peels were prepared by the cellulose acetate peel method (Basinger and Rothwell, 1977; Basinger, 1981) after etching for two minutes in 48% HF. The peels were cleared in clove oil, mounted in Canada Balsam with slide and coverglass. Ground sections were prepared by mounting the wafers on microscope slides with Elmers Epoxy, and grinding to approximately 30 μm thickness on a Buehler thin sectioning machine. Anatomical detail from thin sections was photographed with the Nikon FE camera mounted on a Nikon Labophot compound microscope using standard transmitted and/or reflected light from an obliquely positioned fiber optic source. For one taxon (*Hydrangea*), small organically preserved seeds were liberated by dissolving the silicified fruit in hydrofluoric acid, then washed and mounted on microscope slides for transmitted light microscopy.

External measurements were obtained with brass calipers graduated to 0.1 mm. Dimensions were calculated on the basis of all available specimens, or at least 25 specimens, of each species. Obviously contorted or broken specimens were not included in the measurements. Unless otherwise indicated, the longest axis of the fruit or seed was treated as height or length. Width and thickness are the wider and narrower dimensions, respectively, measured at right angles to the length.

Methods of identifying fossil fruits and seeds are reviewed in detail by Tiffney (1990). Discussions of extant and fossil seeds by Reid and Chandler (1933), Chandler (1961b, 1964, 1978), Collinson (1983), Friis (1985), Kirchheimer (1957), and Mai (1976) provided a useful guide for preliminary investigations of the Clarno taxa. Comparisons with extant seeds were carried out by examining representatives of most extant angiosperm families in herbaria and seed collections.

RESULTS AND INTERPRETATION

SYSTEMATIC DIVERSITY OF THE NUT BEDS FLORA

One hundred and forty five genera and 173 species of fruits and seeds have been recognized among the Nut Beds collections (Table 1) and are described and illustrated in this monograph. In addition, among the less well-preserved specimens in the collections, there may be as many as twenty more genera that are excluded from the following discussions. Four gymnosperm genera, representing Pinaceae and Taxaceae, are recognized, but the majority of taxa are angiosperms. From the working total of 145 genera and 173 species, only 75 genera and 102 species have been identified as belonging to modern families. The remaining taxa, constituting approximately half of the assemblage, are of uncertain affinity with respect to extant families (Text-fig. 5A). This group probably includes both extant and extinct genera, but the affinities are still undetermined at the time of this writing. Nevertheless, these species are described and illustrated in order to document, as completely as possible, the full diversity of the flora and to invite further study by other researchers.

The numbers presented above, based only on the fruits and seeds, understate the full diversity of the Nut Beds flora because many additional taxa are represented by other plant organs. For example, *Equisetum clarnoi* (J. T. Brown, 1975; Retallack, 1981) is known from silicified stems and compressed strobili (Pl. 1, fig. 1); four types of ferns are known from leaves and stems, and a cycad with foliage resembling *Dioon* is present (Manchester, 1981). Families confirmed on the basis of wood that have not been recognized among the fruits and seeds include Ginkgoaceae (*Ginkgo*; Scott et al., 1962), Trochodendraceae (Scott and Wheeler, 1982), and Sterculiaceae (Manchester, 1979, 1980). Although the extent of overlap is unknown, it is probable that the fossil leaves (Manchester, 1981) and woods (Scott and Wheeler, 1982) collected from the Nut Beds represent some of the same species as those known from seeds or fruits treated here. However, because none of the organs have been found in direct attachment, assessments of conspecificity remain speculative.

It is not possible to give a precise percentage of the Nut Beds genera that are extinct vs. extant because a large proportion of the genera are still of uncertain systematic position relative to modern families and genera. Nevertheless, all genera recognized here may be divided into four groups indicating current knowledge of their status relative to living taxa (Text-fig. 5):

1) *Extant genera.* Those that possess features that are diagnostic of a living genus; these species are given the appropriate modern generic name, for example, *Cornus, Magnolia, Meliosma, Quercus.*

2) *Extinct genera.* Those that have features diagnostic of a particular modern family, but with additional characters that set them apart from living genera of that family, for example, *Cruciptera, Langtonia, Pentoperculum.*

3) *Form genera.* Those that have not been traced to a particular modern family (i.e., incertae sedis), for example, *Carpolithus, Joejonesia.* Form genera probably include extant genera that I have failed to identify, as well as extinct genera and/or families. These genera

Table 1.—Comprehensive list of fruit and seed taxa from the Clarno Nut Beds assemblage indicating number of specimens observed.

taxon	*quantity*
Pinaceae	
Pinus sp.	1
Taxaceae	
Taxus masonii sp. nov.	20
Torreya clarnensis sp. nov.	75
Diploporus torreyoides gen. et sp. nov.	3
Actinidiaceae	
Actinidia oregonensis sp. nov.	7
Alangiaceae	
Alangium eydei sp. nov.	33
Alangium rotundicarpum sp. nov.	1
Anacardiaceae	
Pentoperculum minimus (Reid et Chandler) gen. et comb. nov.	62
Rhus rooseae sp. nov.	15
Annonaceae	
Anonaspermum cf. *pulchrum* Reid et Chandler	16
Anonaspermum bonesii sp. nov.	1
Anonaspermum rotundum sp. nov.	1
Araliaceae	
Paleopanax oregonensis gen. et sp. nov.	3
Betulaceae	
Kardiasperma parvum gen. et sp. nov.	21
Coryloides hancockii gen. et sp. nov.	34
Burseraceae	
Bursericarpum oregonense sp. nov.	40
Bursericarpum sp.	6
Cornaceae	
Cornus clarnensis sp. nov.	5
Langtonia bisulcata Reid et Chandler	31
Mastixia sp.	4
Mastixioidiocarpum oregonense Scott	22
Mastixicarpum occidentale sp. nov.	2
Nyssa scottii sp. nov.	6
Nyssa spatulata (Scott) comb. nov.	25
Nyssa sp.	3
Fagaceae	
Castanopsis crepetii sp. nov.	6
Quercus paleocarpa Manchester	3
Flacourtiaceae	
Saxifragispermum tetragonalis sp. nov.	65
Hamamelidaceae	
Fortunearites endressii gen. et sp. nov.	6
Hydrangeaceae	
Hydrangea knowltonii gen. et sp. nov.	45+
Icacinaceae	
Iodeae	
Iodes multireticulata Reid et Chandler	14
Iodes chandlerae sp. nov.	13
Iodicarpa ampla gen. et sp. nov.	15+
Iodicarpa lenticularis sp. nov.	16+
Comicilabium atkinsii gen. et sp. nov.	8
Phytocreneae	
Palaeophytocrene hancockii Scott	20
Palaeophytocrene pseudopersica Scott	80
Pyrenacantha occidentalis sp. nov.	8
Juglandaceae	
Juglandeae	
Cruciptera simsonii (Brown) Manchester	12
Juglans clarnensis Scott	200+
Engelhardieae	
cf. *Palaeocarya clarnensis* Manchester	48+
Platycaryeae	
Paleoplatycarya? *hickeyi* sp. nov.	5
Lauraceae	
Laurocalyx wheelerae sp. nov.	12
Laurocarpum hancockii sp. nov.	1
Laurocarpum nutbedensis sp. nov.	1
Laurocarpum raisinoides sp. nov.	1
Lindera clarnensis sp. nov.	5
Leguminosae	
Leguminocarpon sp.	1
Lythraceae	
Decodon sp.	7
Magnoliaceae	
Magnolia muldoonae sp. nov.	100+
Magnolia paroblonga sp. nov.	17
Magnolia tiffneyi sp. nov.	10
Menispermaceae	
Coscineae	
Anamirta leiocarpa sp. nov.	16
Menispermeae	
Diploclisia auriformis (Hollick) comb. nov.	8
Eohypserpa scottii sp. nov.	2
Davisicarpum limacioides sp. nov.	1
Palaeosinomenium venablesii Chandler	70
Tinosporeae	
Atriaecarpum clarnense sp. nov.	4
Calycocarpum crassicrustae sp. nov.	40
Chandlera lacunosa Scott	40
Curvitinospora formanii gen. et sp. nov.	1
Odontocaryoidea nodulosa Scott	80+
Tinospora elongata sp. nov.	7
Tinospora hardmanae sp. nov.	4
Tinomiscoidea occidentalis sp. nov.	1
Thanikaimonia geniculata gen. et sp. nov.	1
Musaceae	
Ensete oregonense Manchester et Kress	70
Palmae	
Sabal bracknellensis (Chandler) Mai	6
Sabal jenkinsii (Reid et Chandler) comb. nov.	30
Platanaceae	
Macginicarpa glabra Manchester	200+
Platanus hirticarpa sp. nov.	1
Tanyoplatanus cranei gen. et sp. nov.	3
Rosaceae	
Prunus weinsteinii sp. nov.	1
Prunus olsonii sp. nov.	10

Table 1.—Continued.

taxon	*quantity*
Rubiaceae	
Emmenopterys dilcheri sp. nov.	7
Sabiaceae	
Meliosma beusekomii sp. nov.	110
Meliosma bonesii sp. nov.	22
Meliosma elongicarpa sp. nov.	2
Meliosma cf. *jenkinsii* Reid et Chandler	8
Meliosma leptocarpa sp. nov.	50+
Sabia americana sp. nov.	22
Sapindaceae	
Deviacer wolfei gen. et sp. nov.	28
Palaeoallophylus globosa sp. nov.	36
Palaeoallophylus gordonii sp. nov.	20
Sapotaceae	
Bumelia? globosa sp. nov.	40+
Bumelia? subangularis sp. nov.	5
Schisandraceae	
Schisandra oregonensis sp. nov.	27
Staphyleaceae	
Tapiscia occidentalis Manchester	78
Symplocaceae	
Symplocos nooteboomii sp. nov.	4
Theaceae	
Cleyera grotei sp. nov.	32
Ulmaceae	
Celtidoideae	
Aphananthe maii sp. nov.	12
Celtis burnhamae sp. nov.	100+
Celtis sp.	160+
Trema nucilecta sp. nov.	46
Ulmoideae	
Cedrelospermum lineatum (Lesq.) Manchester	11
Vitaceae	
Ampelocissus auriforma sp. nov.	90
Ampelocissus scottii sp. nov.	10
Ampelopsis rooseae sp. nov.	260
Parthenocissus angustisulcata Scott	10
Parthenocissus clarnensis sp. nov.	32+
Vitis magnisperma Chandler	9
Vitis tiffneyi sp. nov.	50+
Incertae Sedae	
Ankistrosperma spitzerae gen. et sp. nov.	48
Anonymocarpa ovoidea gen. et sp. nov.	1
Ascosphaera eocenis gen. et sp. nov.	20
Axinosperma agnostum gen. et sp. nov.	22
Bonesia spatulata gen. et sp. nov.	15
Comminicarpa frusae gen. et sp. nov.	5+
Cuneisemen truncatum gen. et sp. nov.	9
Dentisemen parvum gen. et sp. nov.	3
Durocarpus cordatus gen. et sp. nov.	1
Ferrignocarpus bivalvis gen. et sp. nov.	24
Fimbrialata wingii gen. et sp. nov.	10
Fragarites ramificans gen. et sp. nov.	7
Globulicarpium levigatum gen. et sp. nov.	20
Hexacarpellites hallii gen. et sp. nov.	1
Joejonesia globosa gen. et sp. nov.	1
Lignicarpus crassimuri gen. et sp. nov.	4
Ligniglobus sinuosifibrae gen. et sp. nov.	5
Lunaticarpa curvistriata gen. et sp. nov.	80
Microphallus perplexus gen. et sp. nov.	25
Nephrosemen reticulatus gen. et sp. nov.	21
Omsicarpium striatum gen. et sp. nov.	1
Pasternackia pusilla gen. et sp. nov.	220
Pileosperma minutum gen. et sp. nov.	10
Pileosperma ovatum sp. nov.	35
Pistachioides striata gen. et sp. nov.	2
Pollostosperma dictyum gen. et sp. nov.	260
Polygrana nutbedensis gen. et sp. nov.	3
Pruniticarpa cevallosii gen. et sp. nov.	3
Pteronepelys wehrii gen. et sp. nov.	2
Pulvinisperma minutum gen. et sp. nov.	170
Pyrisemen attenuatum gen. et sp. nov.	32
Quintacava velosida gen. et sp. nov.	1
Sambucuspermites rugulosus gen. et sp. nov.	9
Scabraecarpium clarnense gen. et sp. nov.	9
Scalaritheca biseriata gen. et sp. nov.	10
Scaphicarpium radiatum gen. et sp. nov.	15
Sphaerosperma riesii gen. et sp. nov.	2
Sphenosperma baccatum gen. et sp. nov.	1
Stockeycarpa globosa gen. et sp. nov.	1
Striatisperma coronapunctatum gen. et sp. nov.	69
Tenuisperma ellipticum gen. et sp. nov.	2
Tiffneycarpa scleroidea gen. et sp. nov.	1
Trigonostela oregonensis gen. et sp. nov.	9
Tripartisemen bonesii gen. et sp. nov.	270+
Triplascapha collinsonae gen. et sp. nov.	4
Triplexivalva rugata gen. et sp. nov.	12
Trisepticarpium minutum gen. et sp. nov.	1
Truncatisemen sapotoides gen. et sp. nov.	3
Ulosperma hardingae gen. et sp. nov.	4
Wheelera lignicrustae gen. et sp. nov.	3
Carpolithus bellispermus Chandler	100
Carpolithus sp. 1	2
Carpolithus sp. 2	2
Carpolithus sp. 3	3
Carpolithus sp. 4	1
Carpolithus sp. 5	2
Carpolithus sp. 6	1
Carpolithus sp. 7	3
Carpolithus sp. 8	1
Carpolithus sp. 9	10
Carpolithus sp. 10	4
Carpolithus sp. 11	1
Carpolithus sp. 12	1
Carpolithus sp. 13	1
Carpolithus sp. 15	1
Carpolithus sp. 16	15
Carpolithus sp. 17	1
Carpolithus sp. 18	2
Carpolithus sp. 19	1
Carpolithus sp. 20	1
Carpolithus sp. 21	1
Five-part flower	2
Extant families: 75 genera, 102 species	
Unknown families: 70 genera, 71 species	
Total: 145 genera, 173 species	

include some interesting puzzles for future systematic research.

4) *Stereotype genera*. Those that have features diagnostic of a particular modern family, with a suite of characters found in more than one living genus of that family. Species assigned to stereotype genera cannot be resolved to a single extant or extinct genus; for example, *Anonaspermum*, *Laurocarpum*, *Palaeosinomenium*.

One must be cautious when interpreting fossil generic names. Form genera should not be blanketly assumed to represent extinct genera, because it is just as likely that they may represent undetermined extant genera. Likewise, in the characters available for study, stereotype genera are indistinguishable from two or more extant genera, and accordingly should not be assumed to represent extinct genera.

The Nut Beds biota also includes insect remains. Two types of beetles are known from silicified adults (S. R. Manchester, pers. obs.) and one of the taxa preliminarily thought to be silicified seeds has been determined to represent eggs of the Phasmidae (Sellick, in press). The possibility exists that some of the form genera described in this monograph represent insect eggs or egg cases rather than plant remains. Rather than exclude taxa that could possibly be construed as insect eggs, I believe it is useful to document all of the structures because of the possible importance for biostratigraphy and/or future insect work. As this goes to press, I consider the following taxa worthy of investigation as possible insect remains: *Carpolithus bellispermus*, *Scalaritheca* and *Pileospermum*. These taxa, nevertheless, have been included in the fruit/seed counts and, if ultimately determined to be of insect origin, will slightly alter some of the percentages presented in this section.

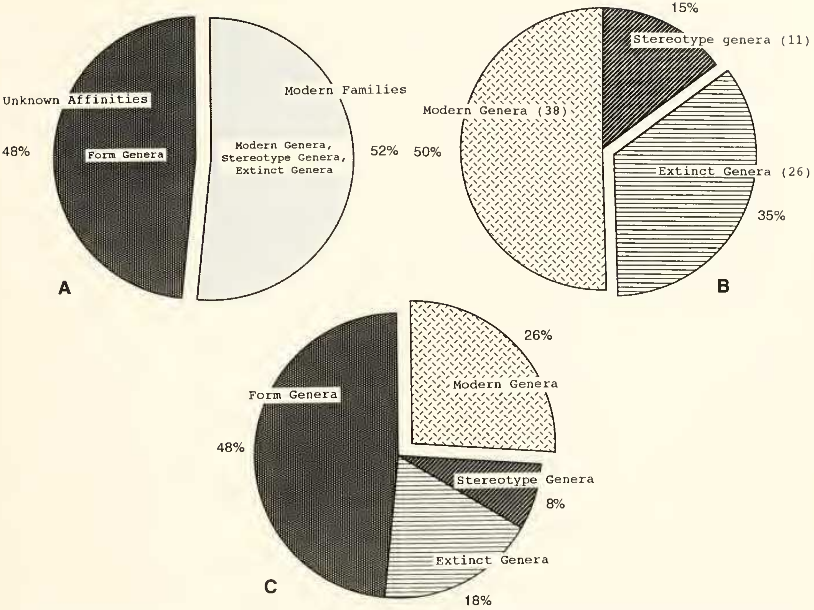
Thirty-five extant families have been recognized among the Nut Beds fruits and seeds. Among the 75 genera of known familial affinities, 38, or 50%, have been attributed to genera that are still living today (Text-fig. 5B). These extant genera, indicated in Tables 1 and 5, are significant in showing little or no evolution in fruit morphology over a period of at least 43 million years. The number of extant genera recognized may be expected to increase with additional work as the affinities of form genera come to light.

At least 26 genera (35% of those for which familial affinities have been determined) are extinct: *Atriaecarpum*, *Cedrelospermum*, *Chandlera*, *Comicilabium*, *Kardiasperma*, *Coryloides*, *Cruciptera*, *Curvitinospora*, *Davisicarpum*, *Deviacer*, *Diploporus*, *Eohypserpa*, *Fortunearites*, *Iodicarpa*, *Langtonia*, *Macginicarpa*, *Mastixicarpum*, *Mastixioidiocarpum*, *Odontocaryoidea*, *Palaeophytocrene*, *Palaeosinomenium*, *Pentoperculum*, *Saxifragispermum*, *Tanyoplatanus*, *Thanikaimonia*, *Tinomiscoidea*. This figure, too, will probably change with additional work. Sometimes fossils initially considered to be extinct are subsequently found to be living as neobotanical exploration and comparative work continues, as in the classic case of *Metasequoia*, and as more recently discovered in *Diplopanax* (Eyde and Xiang, 1991) and *Craigia* (Kvaček, Bůzek and Manchester, 1991). Morphological differences between related fossil and extant taxa that may be viewed as warranting generic distinction by one investigator may be viewed as simply reflecting greater variability within a single genus by another. For example, the species formerly treated as *Palaeonyssa* by Reid and Chandler (1933) and Scott (1954) are herein regarded as *Nyssa*.

Relative to other paleobotanical localities of the Clarno Formation, the Nut Beds fruit and seed assemblage is anomalously high in generic and specific diversity. In surveying the large collections from the lacustrine shales at West Branch Creek (UF loc. 229c, 230, UCMP loc. 3904, USGS loc. 8637), I have observed only 48 distinct types of compressed fruits and seeds and 53 types of leaves.

The leaf flora of the Nut Beds includes about 65 genera—less than half as many as those known from fruits and seeds. Although the leaf collection acquired from the Nut Beds between 1974 and 1981 is the result of more than 2000 person-hours, the recovery process for leaves in the heavily fractured siltstones (Manchester, 1981) is very time-consuming and the total number of leaf specimens is less than 1000. The fruit and seed collections amassed since 1943 include more than 20,000 specimens. Thus, the discrepancies between foliage and diaspore diversity may be in part due to differences in sample size.

It's unlikely that all of the Nut Beds species grew together in the same plant community; rather, it is probable that the assemblage includes elements from various parts of a large watershed. Judging from the sedimentary environment of the Nut Beds and the varying amounts of predepositional erosion evident in the fossil remains, the assemblage probably includes plants from different sources: some local, others carried from various distances upstream. Significant transport of fruits and seeds may also have been effected by birds that consumed fruits from various parts of the forest. When perched on branches close to or overhanging sites of sediment accumulation, birds have the potential to introduce endocarps and seeds from more remote parts of the forest that would otherwise be underrepresented in the fossil assemblage. Such biotic transport, selective for bird-edible fruits, might explain the greater diversity of fruits and seeds than vegetative organs in the Nut Beds. Frugivorous mammals probably also have played a role in fruit dispersal in Eocene



Text-figure 5.—Taxonomic status of Nut Beds fruit and seed genera relative to extant families and genera. A, Proportion of genera identified to modern families vs. those of unknown familial affinities. B, Genera identified to modern families, with proportions of extinct, modern and stereotype genera. C, Summary, emphasizing that only ¼ of genera have been determined to be extant.

forests (Collinson and Hooker, 1992). Indeed, a large proportion of the seeds and endocarps identified appear to have been from drupes or berries that would have been well-suited for bird and/or mammal dispersal. The apparent absence of vitaceous leaf remains in the Clarno collections, contrasted with the abundance and diversity of grape seeds, supports this conclusion.

Growth Habit and Dispersal Ecology

The growth habit of a fossil species, i.e., whether it is a tree, shrub, liana or herb, may be inferred from that of its living relatives. Of course, this means of inference is not applicable to the fruit and seed taxa whose modern affinities are undetermined; therefore, fewer than half of the Nut Beds fruit and seed genera can be analyzed according to this approach. Nevertheless, this methodology gives some insight into the stature of Nut Beds vegetation (Table 2). Among the identified taxa, trees and lianas are particularly well represented, while herbs and aquatic plants are poorly represented.

Many of the fruit and seed genera are deduced to represent trees. Arborescent taxa include *Aphananthe*, *Castanopsis*, Juglandaceae (3 genera), Lauraceae, *Macginicarpa*, *Magnolia*, *Mastixia*, *Meliosma*, *Nyssa*, *Platanus*, *Quercus*, *Sabal*, *Tapiscia*. Trees of lower stature and shrubs probably included Annonaceae, *Cornus*, cycad (known from foliage only), *Fortunearites*, *Taxus*, and *Torreya*. Arborescent taxa can also be inferred independently of fruit and seed data using fossil wood fragments from the Nut Beds. Based on curvature of growth rings, at least 40 different genera were derived from stems larger than 15 cm in diameter and were probably from trees. Some of these woods have been identified, including: *Ginkgo* (Scott et al.,

Table 2.—Present habit and vegetational distribution of Nut Beds genera.

genus	*habit*	*deciduous/ evergreen*	*TRF*	*PTRF*	*NBLE*	*MM*	*MBLD*	*MNH*	*MC*
Actinidia	c	d		+	+	+	+	+	
Alangium	tsc	de	+	+	+	+	+		
Ampelocissus	c	d	+						
Ampelopsis	c	d				+	+		
Anamirta	c	e	+	+					
Aphananthe	t	de	+	+	+	+			
Bumelia	ts	d		+	+				
Calycocarpum	c	d				+			
Castanopsis	ts	e	?	+	+	+	+	+	+
Celtis	t	de	+	+		+		+	+
Cleyera	s	e			+				
Cornus	ts	d			+	+	+	+	
Decodon	s	d			+	+			
Diploclisia	c	e	+[2]	+					
Emmenopterys	t	d				+			
Ensete	h	e	+	+					
Hydrangea	tsc	de	+	+	+	+	+		+
Iodes	c	e	+	+					
Juglans	t	d		+	+	+	+	+	
Lindera	ts	d			+	+		+	+
Magnolia	t	de	+	+	+	+	+	+	
Mastixia	t	e	+[1]						
Meliosma	t	de	+[1]	+	+	+	+	+	
Parthenocissus	c	d				+			
Pinus	t	e	+?	+	+	+	+	+	+
Platanus	t	d	+	+	+	+	?		
Prunus	ts	de			+	+	+	+	+
Pyrenacantha	c	e	+	+	+				
Quercus	t	de	+	+	+	+	+	+	+
Rhus	tsc	de	+[1]	+	+	+			
Sabal	t	e	+	+	+				
Sabia	c	e			+				
Schisandra	c	de			+	+	+		
Symplocos	ts	de	+	+	+	+	+		+
Tapiscia	ts	d				+			
Taxus	t	e			+	+			
Tinospora	c	e	+	+					
Torreya	t	e			+	+			
Trema	ts	e	+	+	+				
Vitis	c	d		+	+	+		+	

[1] Including submontane rainforest.

[2] Including montane forest.

c = climber, s = shrub, t = tree, h = herb, d = deciduous, e = evergreen; TRF = Tropical Rain forest; PTRF = Paratropical Rain forest; NBLE = Notophyllous Broadleaved Evergreen; MM = Mixed Mesophytic; MBLD = Mixed Broadleaved and Deciduous; MNH = Mixed Northern Hardwood; MC = Mixed Coniferous. Vegetation types following Wolfe (1979).

1962), *Tapirira* (Manchester, 1977), Sterculiaceae (Manchester, 1979, 1980), *Alangium*, *Betula*, *Fagaceoxylon*, *Magnolia*, *Plataninium*, *Quercinium*, *Ulminium*, (Scott and Wheeler, 1982), *Engelhardioxylon* (Manchester, 1983), and *Clarnoxylon* (Manchester and Wheeler, 1993).

The diversity of climbers in the flora, at least 22 genera and 30 species, (43% of the 69 species for which growth form may be inferred) is particularly striking. This estimate is based upon extant genera of climbing habit (Table 2), plus extinct genera belonging to families or subfamilies that are virtually all climbers today. Menispermaceae, a family comprised almost exclusively of tropical lianas, is the most diverse family in the Nut Beds fruit and seed assemblage, with 13 genera and 14 species. In addition, seven species of Vitaceae, at least five species of Icacinaceae (those belonging to *Iodes*, *Iodicarpa*, *Palaeophytocrene*, *Pyrenacantha*), and the species of *Actinidia*, *Sabia*, and *Schisandra* probably represent lianas or climbers (Table 2). By contrast with the Nut Beds figure of 43%, the highest known percentages of liana species per flora in extant vegetation are only about 24% (Gentry, 1992).

Lianas such as those of extant Menispermaceae are best developed where the tree canopy is interrupted, for example along stream banks and forest edges (Forman, 1986). Preferential growth at stream side, where seeds may be dropped directly into the sedimentary environment, may have caused over-representation of lianas relative to trees, shrubs and herbs in the fossil assemblage, but I doubt that this bias fully explains the high apparent diversity of lianas. The same families of lianas are also well represented in the Eocene London Clay flora of England (Chandler, 1961b; Collinson, 1983). The diversity of lianas along with the trees mentioned above may be taken as an indication that a multistratal, closed canopy forest had developed (Upchurch and Wolfe, 1987). In addition, Crane (1987) has suggested that lianas and opportunistic shrubs may have played a more dominant role in colonizing bare ground in the Early Tertiary than today because the major radiation of extant angiosperm herbs occurred later in the Tertiary.

Very few of the known Nut Beds taxa represent herbs. Among the fruit and seed genera, *Ensete* is the only known herbaceous element. Stem and leaf records attest to the presence of *Equisetum clarnoi* (Pl. 1, fig. 1) and a few ferns. The ferns are represented by silicified petioles of *Dennstaedtiopsis* and *Acrostichum* and by foliage of *Thelypteris iddingsii* (Knowlton) MacGinitie, and "*Asplenium*" *hurleyensis* Berry (Manchester, 1976). *Lygodium kaulfussii* Heer, which is common at many Clarno localities (Manchester and Zavada, 1987), has not been recovered from the Nut Beds. Floating aquatic plants such as Nymphaeaceae, *Ceratophyllum*, *Trapa* and *Salvinia* are absent. *Decodon*, with a single extant species that grows as a sprawling shrub at the edge of swamps, is the only genus of the Nut Beds flora regarded as semi-aquatic.

A small percentage of the taxa have winged disseminules and were probably wind-dispersed, such as the samaras of *Cedrelospermum*, *Deviacer*, *Cruciptera*, *Palaeocarya*, *Palaeoplatycarya*, and *Pteronepelys*, the tufted achenes of *Platanus* and *Tanyoplatanus*, and the seeds of *Emmenopterys*, *Fimbrialata* and *Hydrangea*. In extant forests, wind-dispersed species tend to best represented among trees and lianas of the forest canopy, while bird-dispersed species are concentrated in the understory (Gentry, 1983). Gentry (1983) also noted that the percentage of species with wind-dispersed diaspores decreases as one proceeds from dry to wet forests in the neotropics.

At least 80% of Nut Beds taxa appear to have been well-suited for biotic dispersal. Nuts that commonly are dispersed by rodents today include *Juglans*, *Castanopsis* and *Quercus* and it may be expected that *Coryloides*, being similar to *Corylus*, was similarly adapted. Although I have not observed obvious gnaw marks on any of the fossil nuts or seeds, it is likely that rodents played some role in seed dispersal. Among the mammalian fauna of the Nut Beds, *Orohippus*, *Hyrachyus* and *Telmatherium* were browsers that may have participated in fruit dispersal. Birds were probably the most important dispersal agents for Nut Beds plants. As inferred from extant relatives and from morphology of the preserved fruit and seed remains, the overwhelming majority of Nut Beds species represent fleshy fruits, of the kind regularly dispersed by birds. Some examples include *Actinidia*, *Anamirta*, Annonaceae, *Aphananthe*, *Celtis*, *Cornus*, *Ensete*, *Mastixia*, *Meliosma*, *Nyssa*, *Prunus*, *Rhus*, *Sabal*, *Symplocos*, *Tapiscia*, *Taxus*, and the seven species of Vitaceae.

Although seed size ranges greatly among the Nut Beds species, the occurrence of many species with large fruits and seeds is particularly striking (Scott, 1954; Tiffney, 1984). Based on a survey of seed size in Cretaceous and Tertiary floras, Tiffney (1984) observed that most angiosperm seeds of the Cretaceous are small; large fruits first become common in the Early Tertiary. The abundance of large fruits in Eocene floras such as the Nut Beds probably coincides both with the radiation of mammal and bird taxa important as dispersal agents, and with the formation of closed canopy forest (Tiffney, 1984). A well-marked correlation between large seed size and establishment in shady, stable plant associations has been statistically documented in living tropical woody plants (Salisbury, 1942; Foster and Janson, 1985; Foster, 1986). In a closed canopy evergreen forest, large seeds have an adaptive advantage over smaller ones because they possess more food reserves for the embryo, enabling the seed to germinate and become established under subdued light conditions. Smaller seeds typically require more intense sunlight for sufficient photosynthesis for a seedling to become established, and are commonly produced in large quantities by plants that are successful at colonizing sun-lit gaps in the forest canopy. The high proportion of relatively large, biotically dispersed fruits and seeds in the Nut Beds assemblage may thus be an indication of closed canopy forest.

CLIMATIC INTERPRETATION

Fossil plants and animals of the Clarno Nut Beds reflect climatic conditions under which the biota existed. The presence of crocodilian teeth and such thermophilic plants as cycads, palms (*Sabal*) and bananas (*Ensete*) gives an indication that the Nut Beds biota lived under typically frost-free, subtropical or tropical conditions. The Middle Eocene coastline was situated only about 100 km to the west (Nilsen and McKee, 1979) so that the Clarno biota probably experienced the moderating climatic influence of the nearby ocean. Deposition of the Clarno Formation took place prior to the Neogene uplift of the Cascade and Coast Ranges that effected the present-day rain shadow.

Paleoclimatic conditions are inferred by identifying floristic and/or physiognomic similarities of a fossil assemblage to a modern vegetation type of known climatic parameters. Discussion of paleoclimate requires a working definition of terms, because different investigators have applied widely differing concepts of what constitutes such categories as tropical, subtropical, and temperate. For consistency with other paleobotanical literature I have adopted the definitions of Wolfe (1979) which are based on modern mean annual temperatures (MAT) for humid to mesic regions of eastern Asia: tropical >25°C; paratropical 20–25°C; subtropical 13–20°C; temperate 10–13°C; paratemperate 3–10°C; subtemperate <3°C. These paramaters, along with mean cold month temperature and mean annual range of temperature, appproximately delimit distinct forest types within mesic vegetation (Wolfe, 1979).

The high proportion of lianas already discussed (43% of the species with known familial affinities) supports previous interpretations that the Nut Beds flora represents tropical or paratropical forest (Scott, 1954; Wolfe 1977), possibly with a multistratal canopy (Upchurch and Wolfe, 1987). Observing that in Recent vegetation, "the great majority of woody lianas are restricted to tropical forests," Gentry (1992) computed the percentage of lianas per florula in temperate eastern North America at 6%, vs. 19% in continental tropical florulas. Gentry's work did not specifically address liana diversity in subtropical or paratropical situations.

Woods from the Nut Beds consistently show growth rings, indicating seasonality of temperature and/or precipitation. However, true ring-porous wood structure, which typically is confined to temperate situations, has not been observed. Of the fruit and seed genera that have been identified to extant genera, at least 42% are deciduous-leaved today (Table 2). Fossil leaves from the Nut Beds are mostly of large size (67% of the dicotyledonous leaf species exceed 10 cm in lamina length) and, at latest count (preliminary to a detailed work on the leaf flora), 33 of the dicot leaf species, or 52%, are entire-margined. Additional research on leaves and woods of the flora may provide physiognomic data useful in testing the taxonomically-based assessment provided here.

One approach to the assessment of paleoclimate is based on the growing conditions of extant taxa related to those identified in the fossil assemblage. The climatic preferences of present-day relatives of the fossil taxa are taken as an indication of the range of conditions under which the fossil flora might have existed. There are various problems inherent in using this uniformitarian approach: 1) the climatic tolerances of a taxon may evolve to accommodate environmental change; 2) the current distribution of a taxon is controlled by many factors, only one of which is regional climate (other important factors include historic barriers to dispersal, and effects of interspecies competition and pathogens); 3) any taxa that are misidentified may introduce erroneous climatic data. Because of problems that may result from mistaken identities, I have been particularly cautious in the systematic treatment of genera in this monograph, placing them in form- or stereotype genera, rather than in the "nearest modern equivalent" when characters diagnostic of a modern genus could not be demonstrated. Despite the limitations of taxonomically based assessments of paleoclimate, such analyses provide at least a coarse guide, and may be used to evaluate conclusions reached by other methods.

Among the Nut Beds taxa that have been identified to Recent genera, most live today within the broad range of temperate to tropical vegetation (Table 2). Some of these, such as *Ampelocissus*, *Anamirta*, *Diploclisia*, *Ensete*, *Iodes*, *Mastixia*, *Pyrenacantha*, and *Tinospora*, are confined to tropical and paratropical vegetation today. Others are elements of temperate forest associations (Mixed Mesophytic and Mixed Broadleaved Deciduous forests, sensu Wolfe, 1979, as modified from Wang, 1961), and are not found in tropical vegetation, e.g., *Cornus*, *Decodon*, *Emmenopterys*, *Fortunearites* (inferred from extant *Fortunearia* and *Sinowilsonia*), *Parthenocissus*, *Tapiscia*, and *Torreya*. Table 2, listing extant genera of the Nut Beds flora and the vegetation types in which they occur today, shows the highest number of taxa (27 of 40 genera) occurring in the Mixed Mesophytic and Mixed Broadleaved Evergreen forest communities, followed by the 24 genera with Paratropical Rain forest affinities, and 22 with Tropical Rain forest affinities. However, if one were to score the extinct genera of Menispermaceae and Icacinaceae as tropical, where these families predominate today, the larger proportion of Nut Beds taxa (37 of 52 genera, or 71%) would be regarded as tropical to paratropical.

Faced with a mixture of taxa, some that are exclusively tropical today and others that are exclusively temperate, interpretation of paleoclimate for the Nut Beds depends on the assumptions made and how the data are weighted. One might, for example, infer a temperate environment for the Nut Beds and suggest that many elements have subsequently evolved into more tropical situations where they are found today. Or, alternatively, the Nut Beds may represent tropical or paratropical vegetation, some of the elements of which have since evolved to accommodate more temperate conditions. The second scenario is favored because tropical to subtropical vegetation is also suggested by foliar physiognomic considerations (Wolfe, 1977; Manchester, 1981). It is also possible that the apparent mixture of cool and warm elements is a genuine reflection of mixed sources, some of the cooler elements having been transported from higher elevations.

Presumably, the presence of frost intolerant taxa places more constraints on the inference of climate than the presence of frost tolerant genera. Although temperate taxa may survive in tropical situations, particularly at higher elevations, tropical elements such as *Ensete*, a member of the banana family, would not be expected to persist in a setting with cold winters. *Ensete* occurs today in paratropical and tropical vegetation of southeast Asia where the mean annual temperature falls within the ranges of 20–25°C (Paratropical Rain forest, sensu Wolfe, 1979) and 25–28°C (Tropical Rain forest sensu Wolfe, 1979), and the mean annual range of temperature is low. The mean annual range of temperature varies from 2–19°C among different weather stations in Paratropical Rain forest and 2–11°C in Tropical Rain forest (Wolfe, 1979). The cold month mean temperature in these vegetation types is 10°C or greater. If it is assumed that its climatic tolerances have not changed significantly since the Eocene, then the presence of *Ensete* suggests warm, moist, equable climate, as is also consistent with the presence of cycads and palms.

The Nut Beds provides just one example of the warm vegetation that was widespread in the Eocene of the northern hemisphere (Wolfe, 1985). Tropical to paratropical vegetation has also been recognized in the Eocene of southern Alaska (Wolfe, 1972, 1977) and in Europe (Reid and Chandler, 1933; Chandler, 1964). A marked temperature decline is apparent by the Early Oligocene, possibly corresponding to changes in ocean currents effected by the Late Eocene separation of South America from Antarctica resulting in development of the circum-Antarctic current (Kennett, 1977; Parrish, 1987) and the formation of deep water channels enabling southward drainage of Arctic Ocean waters caused by the rifting of Spitzbergen and Iceland from Greenland (McKenna, 1975; B. LePage, pers. comm., 1992).

BIOGEOGRAPHIC CONSIDERATIONS

The Nut Beds flora contributes a wealth of data useful in phytogeographic investigations. Floristic comparison, both with other Tertiary floras and with extant floras, provides insight into the spread of boreotropical forest in the Northern hemisphere. This section considers the levels of taxonomic similarity of the Nut Beds flora with other fossil fruit and seed assemblages and with living floras. Comparison with other Tertiary floras indicates particularly close similarity with the Eocene flora of western Europe. Among modern-day vegetation, the closest taxonomic resemblance is found in eastern Asia.

Comparison with other Fossil Floras

Because of the high proportion of Nut Beds genera that are extinct and/or of indeterminate familial affinity, it is not possible to link each of the fossil fruit/seed species with a corresponding leaf species. Therefore, the most informative paleofloristic comparisons are those made with other fossil fruit and seed assemblages. Detailed comparison with other Paleogene leaf floras will become possible when the leaf assemblages of the Nut Beds and other Clarno localities are documented.

North American Fossil Floras

The Late Eocene or Early Oligocene LaPorte flora of northern California, best known for its leaf assemblage (Potbury, 1935), has recently yielded a good collection of well-preserved, lignitized fruits and seeds, many of which are shared at the generic, and possibly specific, levels with Nut Beds taxa. A preliminary taxonomic list of LaPorte fruit and seed flora was presented by Tiffney (in Doyle et al., 1988) along with an identification key and illustrations (those taxa indicated by asterisks (*) are shared with the Nut Beds flora): *Dracontomelon* type [probably *Pentoperculum**], hamamelidaceous seed*, *Quercus**, *Pterocarya/Cyclocarya* type, *Magnolia*?*, *Mastixia* (*Ganitrocera* type)[probably *Mastixioidiocarpum**], *Odontocaryoidea* type*, *Stephania* type [similar to *Palaeosinomenium**], *Tinospora* type*, *Nyssa**, *Rhamnus*?, *Zanthoxylum*, Sapotaceae*, *Tapiscia*?*, *Halesia*?, *Symplocos**, *Vitis**, *Parthenocissus**. It is noteworthy that the Nut Beds flora bears greater similarity to this younger flora than to other Middle Eocene fruit and seed assemblages in North America.

The Middle Eocene Princeton chert flora of southern British Columbia, Canada includes a variety of anatomically preserved fruits and seeds that are revealed by sectioning and peeling the chert (Basinger and Rothwell, 1977; Cevallos-Ferriz and Stockey, 1988a, 1988b, 1989, 1990, 1991). The flora is relatively low in diversity, but includes several taxa in common with the Nut Beds flora, including Vitaceae (Cevallos-Ferriz and Stockey, 1989), Lauraceae, sabaloid Palmae (Erwin, 1987), *Decodon* (Cevallos-Ferriz and Stockey, 1988a), *Prunus* (Cevallos-Ferriz and Stockey, 1991), a mastixioid species similar to *Mastixicarpum* (Stockey, pers. comm., 1990), and the newly recognized *Stockeycarpa* (p. 111). The Princeton flora includes aquatic plants such as Nympheaceae (Cevallos-Ferriz and Stockey, 1989), which are unknown from the Nut Beds, and appears to lack the diversity of lianas characteristic of the Nut Beds assemblage. *Metasequoia*, which is abundant in the Princeton flora (Basinger, 1981) is absent from the Clarno Formation, though it becomes abundant in the Lower Oligocene of the overlying John Day Formation (Manchester and Meyer, 1987). The full diversity of the Princeton flora remains to be documented so I hesitate to provide statistical comparison between the Princeton and Nut Beds floras. However, the presence of several shared genera indicates that the geographic ranges of some of the Nut Beds taxa extended into the northern part of the continent.

Although it is known mostly from leaf impressions, the Middle Eocene (Lower Ravenian) assemblages of the Kushtaka and Kulthieth Formations in the Gulf of Alaska appear to be floristically very similar to the Nut Beds assemblage (Wolfe, 1972, 1977). Shared or similar genera include *Alangium*, *Anamirta*, *Diploclisia*, *Limacia* (cf. *Davisicarpum*), *Mastixia*, *Meliosma*, *Palaeophytocrene*, *?Pyrenacantha*, *Sabalites*, and *Vitis*. These assemblages are similar to the Nut Beds flora in the high proportion of lianas. Geophysical and paleobotanical data suggest that the Gulf of Alaska floras are part of a tectonic block that was located farther south in the Eocene (Cowan, 1982; Saleeby, 1983; Axelrod, et al., 1991).

In the southeastern United States, the Middle Eocene Claiborne flora of Tennessee and Kentucky is best known for fossil leaves (Berry, 1930; Dilcher, 1971), but has also yielded about 90 distinct taxa of fruits and seeds (Grote, 1989). Given the similarity in age, one might expect a high percentage of taxa to be shared between the Clarno and Claiborne floras. Although some of the same families are present, e.g., Annonaceae, Hamamelidaceae, Juglandaceae, Leguminosae, Magnoliaceae, Sapotaceae, and Theaceae, generic similarity is minimal, including only *Magnolia* (Grote, 1989), *Nyssa* (Dilcher and McQuade, 1967), *Palaeocarya* (Dilcher, Potter and Crepet, 1976; Manchester, 1987), and *Sabal* (represented by leaves, Daghlian, 1978). Unlike the Nut Beds flora, the Claiborne includes a large number of taxa with present-day relatives in tropical America (Roth and Dilcher, 1979; Taylor, 1990). The Clarno flora lacks the high diversity of legumes found in the Eocene of southeastern North America (Herendeen and Dilcher, 1990; Herendeen, 1992). The apparent absence in the Claiborne flora of families that are diverse in the Clarno flora, such as Icacinaceae, Menispermaceae and Vitaceae, is conspicuous. These differences suggests major floristic discontinuity between northwestern and southeastern North America in the Middle Eocene. The floristic differences between the Clarno and Claiborne assemblages might be due in part to climatic and edaphic factors, but may also reflect barriers to dispersal, including the prior mid continental sea of the Cretaceous and rise of the Rocky Mountains. High paleoelevations that have been inferred for the southern Rocky Mountains by the Late Eocene (Meyer, 1992) may have reinforced floristic differentiation of western and eastern Eocene floras of North America.

The Brandon Lignite flora of Vermont is relevant in this comparison as the only well-documented Tertiary megafossil flora of northeastern North America. Although not independently dated, the flora is thought to be Oligocene (Tiffney, 1981) or perhaps Early Miocene (Tiffney, 1985b). The Brandon flora appears to lack tropical elements such as Menispermaceae and Icacinaceae. Genera shared with the Nut Beds include *Alangium* (Eyde, Bartlett and Barghoorn, 1969), *Magnolia* (Tiffney, 1977), *Vitis* and *Parthenocissus* (Tiffney and Barghoorn, 1976), *Nyssa* (Eyde and Barghoorn, 1963), and *Symplocos* (from pollen, Traverse, 1955; from endocarps, Tiffney, pers. comm., 1992). The composition and geographic placement of the Brandon flora provide support for the concept of a Tertiary land connection across the North Atlantic (Tiffney, 1985b).

European Fossil Floras

Most of the families and many of the genera present in the Nut Beds are also known from the Eocene of Europe (Text-fig. 6). Comparable floras include the Early Eocene London Clay of southern England and the Middle Eocene Geiseltal and Messel floras of Germany (Table 3). The largest and most intensively investigated of these, with about 200 described genera of fruits and seeds, is the London Clay (Reid and Chandler, 1933; Chandler, 1961b, 1964, 1978; Collinson, 1983). The London Clay assemblage includes pyritized fruits and seeds collected from several localities of the London Clay Formation along the southern coast of England. The London Clay fossils were deposited in marine sediment, and include disseminules of mangrove vegetation and shark teeth that are absent in the Nut Beds. However, most of the London Clay plants are terrestrial, evidently deposited near the mouth of a large river, and provide a good record of regional vegetation.

Similarity between the Clarno and London Clay floras was recognized previously on the basis of preliminary investigation of the Nut Beds assemblage and has contributed to the concept of an Eocene boreotropical flora (Scott, 1954; Chandler, 1964; Wolfe, 1975; Tiffney, 1985b; Mai, 1989). It is now possible to quantify the level of similarity based on the entire Nut Beds fruit and seed collection. Of the 145 fruit and seed genera currently recognized from the Nut Beds assemblage, 30 genera (20%) are shared with the London

Clay flora (Table 3; Text-fig. 6). In addition, about 15 species (10%) are the same or are nearly indistinguishable from those of the London Clay. These data corroborate other evidence for the existence of a land-connection between Europe and North America during the Early Tertiary (McKenna, 1975; Tiffney, 1985a, b). Dated as Early Eocene (Collinson and Hooker, 1987) the London Clay biota predates the Middle Eocene Nut Beds biota by about five million years. The timing, routes and rate of dispersal of individual taxa across land connection(s) between western Europe and western North America are not well understood, but the younger age of the Nut Beds deposit indicates that the interchange of these taxa between Europe and North America must have occurred during or prior to the Middle Eocene.

Fruit and seed floras of central Europe are not as diverse, or have not been as thoroughly documented, as the London Clay flora, but include additional taxa shared with the Clarno flora. The Middle Eocene Geiseltal flora from extensive lignite deposits in eastern Germany includes well-preserved leaves (Rüffle, 1976), pollen (Krützsch, 1976) and fruits and seeds. Mai (1976) recognized 25 genera and 28 species of fruits and seeds from the Geiseltal, nine of which are shared with the Nut Beds: *Castanopis*, *Iodes*, *Magnolia*, *Meliosma*, *Nyssa*, *Pinus*, *Sabal*, *Tapiscia*, and *Alangium*. The Middle Eocene Messel flora in western Germany (Schaarschmidt, 1988) is a lacustrine deposit that includes well-preserved compressions of leaves (Wilde, 1989), and fruits and seeds (Collinson, 1982, 1988). About fifty genera of fruits and seeds are present in the collections from Messel, about one quarter of which are shared with the Nut Beds. The shared genera include *Cruciptera*, *Iodes*, *Magnolia*, *Mastixia*, *Meliosma*, *Palaeocarya*, *Palaeophytocrene*, *Palaeosinomenium*, *Pentoperculum*, *Prunus*, *Tapiscia*, *Tinospora*, *Vitis*?, and *Tripartisemen* (Collinson, 1982, 1988 and pers. obs.)[2]. Of these, *Palaeocarya*, *Tripartisemen* ("?Lythraceae" in Collinson, 1988) and *Cruciptera* (Manchester, 1991) are not recorded from the London Clay.

Combining data from the London Clay, Messel and Geiseltal floras (Table 3), the percentage of Nut Beds genera shared with the Early to Middle Eocene of Europe is 24. Some of the Nut Beds taxa have not been recorded from the Early and Middle Eocene of Europe but are known from later Tertiary deposits. Examples include *Actinidia* (Kirchheimer, 1957; Friis, 1985), *Cedrelospermum* (Manchester, 1987b, 1989a)[2], *Celtis* (Manchester, 1989c), *Decodon* (Friis, 1985), *Hydrangea* (Mai, 1985), *Rhus* (Friis, 1969), and *Sabia* (Geissert and Gregor, 1981). Most of these are no longer native to Europe, having succumbed to Plio-Pleistocene climatic cooling.

Text-figure 6.—Nut Beds fruit and seed genera shared with Eocene floras of Europe. Genera listed in Table 3.

Paleogeography

The geographic routes of exchange between the Nut Beds flora and the London Clay, Messel and Geiseltal floras of western and central Europe are of considerable phytogeographic interest (Tiffney, 1985a, b). Geophysical data suggest that land bridges were open both across the North Pacific and across the North Atlantic during the Eocene (Parrish, 1987). If the connection was across Beringia, then one would expect to see marked floristic similarities with the Eocene of Asia. Although floristic ties with the Recent flora of eastern Asia are strong (discussed next section), the antiquity of this connection needs to be documented. In this regard, it would be desirable to make detailed comparisons with floras of similar age in Asia. However, I am not aware of comparable Asian Eocene fruit and seed floras. Careful comparisons among leaf and pollen records are needed for a better understanding of the similarities and differences between North American and Asian Eocene floras, a project beyond the scope of the present study.

Even if taxa were successful in spreading between North America and Asia via Beringia, the Turgai seaway that separated Asia and Europe through at least the Early Eocene may have blocked exchange with Europe (Tiffney, 1985b). Exchange across the North Atlantic via connections through Greenland and Iceland is viewed as more likely (McKenna, 1975; Tiffney, 1985b), but Early Tertiary floras so far studied from Greenland and Spitzbergen give no clue to the presence of such thermophilic taxa as Menispermaceae and Icacinaceae.

Comparison with Recent Floras

The only genera of the Nut Beds flora that are still native to Oregon today are *Pinus*, *Taxus*, *Celtis*, *Cor-*

---

[2] *Cedrelospermum* is now also recognized at Messel. See Notes added in proof, p. 200.

Table 3.—Clarno fruit and seed taxa shared with European Eocene floras.*

Alangiaceae	
Alangium	LC, G
Anacardiaceae	
Pentoperculum	LC
Annonaceae	
Anonaspermum	LC
Burseraceae	
Bursericarpum	LC
Cornaceae	
Cornus	LC
Langtonia	LC
Mastixia	LC, M
Nyssa	LC, G
Fagaceae	
Castanopsis	G
Flacourtiaceae	
Saxifragispermum	LC
Icacinaceae	
Iodes	LC, G, M
Palaeophytocrene	LC, M
Juglandaceae	
Cruciptera	M
Palaeocarya	LC?, M
Lauraceae	
Laurocalyx	LC
Laurocarpum	LC
Magnoliaceae	
Magnolia	LC, G, M
Menispermaceae	
Atriaecarpum	LC
Davisicarpum	LC
Diploclisia	LC
Eohypserpa	LC
Palaeosinomenium	LC, M
Tinospora	LC, M
Tinomiscoidea	LC
Palmae	
Sabal	LC, G
Rosaceae	
Prunus	M
Sabiaceae	
Meliosma	LC, G, M
Sapindaceae	
Palaeoallophylus	LC
Staphyleaceae	
Tapiscia	LC, G, M
Symplocaceae	
Symplocos	LC
Theaceae	
Cleyera	LC
Vitaceae	
Vitis	LC, M
Ampelopsis	LC
Parthenocissus	LC
Incertae Sedis	
Carpolithus bellispermus	LC
Tripartisemen	M

LC = London Clay; G = Geiseltal; M = Messel. * See also Notes added in proof, p. 200.

nus, and *Quercus*. The majority of extant genera of the Nut Beds flora are found today in other geographic regions. Table 4 and Text-fig. 7 show the distribution of Recent genera known from the Nut Beds in selected modern phytogeographic provinces (southeast Asia, Malesia, western North America, Central America, South America, Europe and Africa). Strongest ties are with Southeast Asia and Malesia.

Within the Americas, the closest floristic ties are with eastern North America and with central America. Twenty-three genera, or 56% of the extant genera known from the Nut Beds, occur in eastern North America. Although most of these occur in other continents as well, *Calycocarpum* and *Decodon* are endemic to eastern North America. Twenty-two genera, or 54%, live today in Central America. However, none of these are presently endemic to the region. *Sabal*, distributed in the southeastern U.S. and tropical America, is one of the few genera of the Clarno assemblage that is limited to the New World in its present-day distribution. The genus was formerly more widespread, however, with Eocene records in Europe (e.g., Mai, 1976) and Asia (Huzioka and Takahasi, 1970).

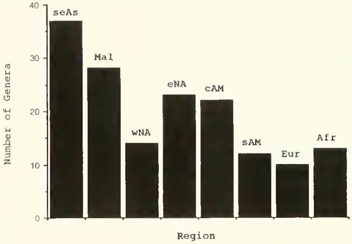
Twenty-four percent of the Nut Beds genera occur today in Europe, although none are endemic there. This percentage, although significantly less than those computed for the present-day floras of southeastern Asia, Malesia, southeastern North America and central America (Table 4), matches that presented above in comparing the Nut Beds flora with Early to Middle Eocene floras of Europe (24%). However the similarity of these values for Eocene and Recent flora of Europe probably is an artifact of the quantitative analysis. All 152 genera, both extinct and extant, are included in the base number for comparing fossil assemblages, whereas only the 41 extant genera form the basis of comparison with the Recent flora. It is important to note that although 36 of the Nut Beds genera are shared with the Eocene flora of Europe, only ten are found in Europe today. Many of the extant genera shared between the Clarno and the London Clay floras are now absent from Europe and are disjunct between Asia and eastern North America and/or central America, for example, *Nyssa*, *Hydrangea*, *Symplocos*; and others are endemic to southeastern Asia.

The strongest geographic affinities are with southeastern Asia (Indochinese Region, sensu Takhtajan, 1986) and Malesia (Malesian Region, sensu Takhtajan,

Table 4.—Present geographic distribution of extant genera represented in the Nut Beds flora.

genus	*seAs*	*Mal*	*wNA*	*eNA*	*cAm*	*sAm*	*Eur*	*Afr*
Actinidia	x	x						
Alangium	x	x						x
Ampelocissus	x	?			x			?
Ampelopsis	x	?		x				
Anamirta	x	x						
Aphananthe	x	x			x			x
Bumelia				x	x	x		
Calycocarpum				x				
Castanopsis	x	x	x					
Celtis	x	x	x	x	x	x	x	x
Cleyera	x				x			
Cornus	x	x	x	x	x	x	x	x
Decodon				x				
Diploclisia	x	x						
Emmenopterys	x							
Ensete	x	x						x
Hydrangea	x	x		x	x	x		
Iodes	x	x						x
Juglans	x		x	x	x	x	x	
Lindera	x	?		x				
Magnolia	x	x		x	x			
Mastixia	x	x						
Meliosma	x	x			x	x		
Nyssa	x	x		x	x			
Pathenocissus	x		x	x	x			
Pinus	x	x	x	x	x	x	x	x
Platanus	x		x	x	x		x	
Prunus	x		x	x	x		x	x
Pyrenacantha	x	x						x
Quercus	x	x	x	x	x	x	x	
Rhus	x	x	x	x	x	x	x	x
Sabal				x	x	x		
Sabia	x	x						
Schisandra	x	x		x				
Symplocos	x	x	x	x	x	x		
Tapiscia	x							
Taxus	x	x	x	x	x		x	
Tinospora	x	x						x
Torreya	x	?	x	x				
Trema	x	x			x	x		x
Vitis	x		x	x	x		x	x
Totals	37	25	14	23	22	12	10	13

seAs = Southeast Asia; Mal = Malesia; eNA = eastern North America; sAm = South America; Eur = Europe; Afr = Africa.



Text-figure 7.—Present geographic distribution of Extant Nut Beds genera. Abbreviations and data from Table 4.

1986). Among Recent floras, the highest number of genera shared with the Nut Beds assemblage is found in eastern Asia. Thirty-seven genera, or 90%, are native to southeastern Asia. The flora of Malesia shares 25 genera with the Nut Beds. Genera that are exclusively Asian or Malesian today include *Actinidia*, *Mastixia*, *Anamirta*, *Sabia*, *Tapiscia*. Although *Meliosma* occurs in central and South America as well as in Asia, four of the Nut Beds species conform most closely to subgenus *Meliosma*, section *Meliosma*, which is exclusively oriental in its Recent distribution (Van Beusekom, 1971). The close floristic similarity with southeastern Asia and Malesia probably reflects the status of this area as a refugium for once-widespread thermophilic genera that could not withstand the effects of climatic cooling and glaciation at the end of the Tertiary in other parts of the northern hemisphere.

INTRODUCTION TO SYSTEMATIC PALEONTOLOGY

New species and genera have been named according to procedures required by the International Code of Botanical Nomenclature (Greuter, 1988). In order for a new species to be validly published, the new name must be accompanied by a description *or* diagnosis (art. 32.1). Fossil plants are excluded from the requirement that the diagnosis be written in Latin (art. 36.1). A new genus and species may be created, and the names of a genus and a species may be simultaneously validated, by provision of a single description or diagnosis (art. 42.1). I have therefore given a combined generic and specific description for the many new, currently monotypic, genera presented here. Type and cited specimens are housed in the indicated museum collections. Specimens are cited as holotypes, paratypes, lectotypes and syntypes as defined in the Botanical Code of Nomenclature (Greuter, 1988). In addition, specimens that are not a part of the original description of species, but which are helpful in understanding the species may be designated hypotypes, as defined previously in zoological (Schenk and McMasters, 1956) and paleobotanical (e.g., MacGinitie, 1953, p. 79) literature.

In naming species of fruits and seeds in this work, I have tended toward conservatism, and have probably erred more on the part of lumping than splitting. By contrast, I consider that the classic monographs on the London Clay flora (e.g., Reid and Chandler, 1933; Chandler, 1978) reflect a greater tendancy for taxonomic splitting. An important objective has been to document the major taxonomic groups represented, thereby highlighting taxa available to the research community for more detailed individual systematic investigations. Many of the extant families and genera recognized have never been analyzed by cladistic methodology, and may be in need of revision. In attempting to classify the entire fossil flora, however, it has been necessary to accept the taxonomic treatments currently available, rather than attempting to revise intrafamilial classifications.

Species are assigned to a modern genus only when sufficient diagnostic characters are present to rule out affinities with other extant genera and/or families. Other species are assigned to extinct, form, or stereotype genera according to the criteria set out on pp. 17–18.

In paleobotanical literature, the generic name *Carpolithus* Schlotheim traditionally has been used as a catchall for fossil fruits and seeds of unknown systematic affinities (Andrews, 1970). Different "species" of *Carpolithus* are often so different from one another that they probably represent different biological genera and families. I have given unique generic names to most of the form genera described from the Nut Beds but have placed an additional 21 taxa as unnamed species of *Carpolithus*. Thus, in comparing the generic diversity of different fossil localities, it is important to be mindful of the hidden diversity lurking under the name *Carpolithus*. It should also be noted that different species assigned to stereotype genera such as *Laurocarpum* and *Anonaspermum* may in reality represent different genera, but information from other plant organs would be required to determine the "real" generic diversity represented by such taxa.

Although leaves and woods co-occur with the fruits and seeds at the Nut Beds locality, no actual attachments have been found, and the high floral diversity combined with the large allochthonous component of the flora makes it difficult or impossible to determine which of the woods, leaves and reproductive structures might be conspecific. Therefore, I have refrained from assigning the same epithet to different isolated organs. It is conceptually intriguing to reconstruct fossil "whole-plant species" from their isolated organs; such reconstructions cannot be *proven* correct, however, unless there are specimens preserving direct attachment between the organs. In some instances evidence of co-occurrence at numerous localities and shared modern familial affinity of isolated organs provides good evidence to infer that particular species of leaves and reproductive structures were perhaps produced by the same biological species, as in the case of the Clarno plane tree (Manchester, 1986). In the discussion accompanying each family of fruit or seed recognized here, I indicate known records based on other organs from the Clarno Formation, recognizing that some of them could in reality represent the same biological species.

ORGANIZATION

The descriptive systematic section is organized into two parts: The first part includes genera that can be confidently assigned to extant plant families. These are arranged alphabetically by family, treating the gymnosperms first, followed by the angiosperms. The second part treats genera of uncertain familial affinity, ordered alphabetically, followed by a numerical sequence of species informally attributed to *Carpolithus*. Families have been organized alphabetically, rather than phylogenetically, because there is more agreement among botanists as to the sequence of the alphabet than to the best phylogenetic arrangement. Phylogenetic schemes are subject to continual change and refinement and, while clearly important in expressing current views of relationships, are cumbersome and unstable as indexing systems. Table 5 presents a phylogenetically arranged list of the Nut Beds fruit and seed genera following, with some modification, the arrangement of Cronquist (1981). Unless otherwise indicated, the numbers for species diversity and the geographic ranges of extant genera were obtained from Mabberley, 1989.

TERMINOLOGY

Geometric symmetry, in particular reflectional point symmetry (Lockwood and MacMillan, 1978), has proven very useful in describing the three-dimensional shapes encountered among fruits and seeds. An object is said to be *bilaterally symmetrical* if there is a single plane of mirror symmetry. Following the same logic, I have used the term *quadrilaterally symmetrical* when there are two planes of mirror symmetry. These two planes usually intersect at right angles along the long axis of the fruit.

In describing the fossil seeds, I have generally used the term seed coat, rather than testa or tegmen, because the terms testa and tegmen have been used in a restricted sense that implies knowledge of ontogeny (Corner, 1976; Schmid, 1986). Seed coat is a neutral descriptive term for the wall of the seed, whereas the terms tegmen and testa (sensu Corner, 1976) require an interpretation that is better left to discussion. Likewise, for fruits, I have applied the term endocarp in a loose sense to refer to the hard, inner layer of the fruit, regardless of its ontogenetic derivation. It is this hard layer of the pericarp (fruit wall) that is most often preserved in the fossil specimens, although occasionally the meso- and exocarp are preserved. Cell layers

Table 5.—Systematic list of Nut Beds genera with known modern familial affinities. Angiosperms listed in phylogenetic sequence similar to that of Cronquist (1981).

- Gymnospermae
  - Order Coniferales
    - Family Taxaceae
      - Genus *Taxus*
      - *Torreya*
      - *Diploporus*
    - Family Pinaceae
      - Genus *Pinus*
- Angiosperms
  - Class Dicotyledonae
    - Subclass Magnoliidae
      - Order Magnoliales
        - Family Magnoliaceae
          - Genus *Magnolia*, 3 spp.
        - Family Annonaceae
          - Genus *Anonaspermum*, 3 spp.
      - Order Laurales
        - Family Lauraceae
          - Genus *Lindera*
          - *Laurocalyx*
          - *Laurocarpum*, 3 spp.
      - Order Illiciales
        - Family Schisandraceae
          - Genus *Schisandra*
      - Order Ranunculales
        - Family Menispermaceae
          - Genus *Anamirta*
          - *Atriaecarpum*
          - *Calycocarpum*
          - *Chandlera*
          - *Curvitinospora*
          - *Davisicarpum*
          - *Diploclisia*
          - *Eohypserpa*
          - *Odontocaryoidea*
          - *Palaeosinomenium*
          - *Tinospora*, 2 spp.
          - *Tinomiscoidea*
          - *Thanikaimonia*
        - Family Sabiaceae
          - Genus *Meliosma*, 5 spp.
          - *Sabia*
    - Subclass Hamamelidae
      - Order Hamamelidales
        - Family Platanaceae
          - Genus *Macginicarpa*
          - *Platanus*
          - *Tanyoplatanus*
        - Family Hamamelidaceae
          - Genus *Fortunearites*
      - Order Urticales
        - Family Ulmaceae
          - Genus *Aphananthe*
          - *Celtis*, 2 spp.
          - *Trema*
          - *Cedrelospermum*
      - Order Juglandales
        - Family Juglandaceae
          - Genus *Juglans*
          - *Cruciptera*
          - cf. *Palaeocarya*
          - *Paleoplatycarya?*
      - Order Fagales
        - Family Fagaceae
          - Genus *Quercus*
          - *Castanopsis*
        - Family Betulaceae
          - Genus *Coryloides*
          - *Kardiasperma*
    - Subclass Dilleniidae
      - Order Theales
        - Family Actinidiaceae
          - Genus *Actinidia*
        - Family Theaceae
          - Genus *Cleyera*
      - Order Violales
        - Family Flacourtiaceae
          - Genus *Saxifragispermum*
      - Order Ebenales
        - Family Sapotaceae
          - Genus *Bumelia*?, 2 spp.
        - Family Symplocaceae
          - Genus *Symplocos*
    - Subclass Rosidae
      - Order Rosales
        - Family Hydrangeaceae
          - Genus *Hydrangea*
        - Family Rosaceae
          - Genus *Prunus*, 2 spp.
      - Order Fabales
        - Family Leguminosae
          - Genus *Leguminocarpon*
      - Order Myrtales
        - Family Lythraceae
          - Genus *Decodon*
      - Order Cornales
        - Family Alangiaceae
          - Genus *Alangium*
        - Family Cornaceae
          - Genus *Cornus*
          - *Langtonia*
          - *Mastixia*
          - *Mastixioidiocarpum*
          - *Mastixicarpum*
          - *Nyssa*, 3 spp.
      - Order Celastrales
        - Family Icacinaceae
          - Genus *Paleophytocrene*, 2 spp.
          - *Iodes*, 2 spp.
          - *Pyrenacantha*
          - *Comicilabium*
          - *Iodicarpa*, 2 spp.
      - Order Rhamnales
        - Family Vitaceae
          - Genus *Ampelocissus*, 2 spp.
          - *Ampelopsis*
          - *Parthenocissus*, 2 spp.
          - *Vitis*, 2 spp.
      - Order Sapindales
        - Family Staphyleaceae
          - Genus *Tapiscia*
        - Family Sapindaceae
          - Genus *Palaeoallophylus*, 2 spp.
          - *Deviacer*
        - Family Burseraceae
          - Genus *Bursericarpum*, 2 spp.
        - Family Anacardiaceae
          - Genus *Pentoperculum*
          - *Rhus*
      - Order Apiales
        - Family Araliaceae
          - Genus *Paleopanax*
    - Subclass Asteridae
      - Order Rubiales
        - Family Rubiaceae
          - Genus *Emmenopterys*
  - Monocotyledons
    - Subclass Arecidae
      - Order Arecales
        - Family Palmae
          - Genus *Sabal*, 2 spp.
    - Subclass Zingiberidae
      - Order Zingiberales
        - Family Musaceae
          - Genus *Ensete*

may be described as uni-, bi-, or multi*seriate*, indicating the thickness of the layer in numbers of cells. The orientation of cells relative to the seed or fruit surface morphology may also be important. Cells are oriented *anticlinally*, if their long axes are perpendicular to the trend of the adjacent external or internal surface. Cells are oriented *periclinally* if their long axes are parallel to the trend of the adjacent external or internal surface. Periclinally oriented cells may at the same time be horizontally or vertically oriented with respect to the principal axis of the fruit or seed.

MEASUREMENTS

If a species is known from three or fewer specimens, then the individual measurements of each are listed in the description. If more than three are measured, then the range, mean (avg.) and standard deviation (SD) are presented followed by the number of specimens measured (n). Broken specimens vary in completeness and sometimes provide only one or two of the three spatial dimensions (length, width and/or thickness), hence, the number of measurement indicated for length may differ from those given for width and/or thickness.

ABBREVIATIONS

Specimen numbers are prefixed by the appropriate institutional abbreviation, indicating where the specimen is deposited. The largest collections are at the US National Museum (USNM), Washington D.C. and the Florida Museum of Natural History, Gainesville (UF). Additional smaller collections were studied at the University of California Museum of Paleontology, Berkeley, California (UCMP), the University of Michigan Museum of Paleontology, Ann Arbor, Michigan (UM), Harvard University, Cambridge, Massachusetts (HU), the Burke Memorial Washington State Museum, University of Washington, Seattle (UWBM), and the Oregon Museum of Science and Industry, Portland (OMSI). Reference is also made to fossils from other localities deposited at the Natural History Museum, London (BM) and the Peabody Museum of Yale University, New Haven (YPM) and to extant seeds from the National Seed Herbarium of the Beltsville Agricultural Research Center, Beltsville, Maryland (BARC), the herbaria of the Smithsonian Institution, Washington, DC (US), Missouri Botanical Garden (MO), Rijksherbarium, Leiden (L), University of Florida (FLAS) and the Arnold (A) and Gray (GH) herbaria of Harvard University, Cambridge, Massachusetts.

The authors' names for families, genera and species are presented at the first occurrence in the text, and may be abbreviated. Standard abbreviations for the names of botanists are presented in Mabberley (1989, pp. 661–706).

In the plate captions, the abbreviations preceding the magnification refer to techniques used in photography. "PC", or palladium-coated, is indicated for specimens that were coated to enhance reflected light microscopy (see materials and methods). "TL" refers to transmitted light microscopy, and "RL" to reflected light micrography, while "SEM" denotes scanning electron microscopy. When not specified, specimens were photographed by reflected light, generally with the light source from the upper left and lower right.

Family **PINACEAE** Lindley

Genus **PINUS** L.

Pinus sp.

Plate 1, figures 6–9

Description.—Pollen cone elongate, with central axis 1.2 mm thick surrounded by numerous helically arranged sporophylls, about 30 sporophylls per cycle; cone width 5.2 mm, length more than 12 mm (specimen incomplete); lower part of cone with a bulge formed by large curved scales 4.5–5.5 mm long; sporophylls 1.5–1.8 mm long, thickened and upcurved distally; pollen sacs paired, abaxial on each sporophyll, 0.7–0.8 mm long.

Specimen.—UF 9334.

Discussion.—Although no seeds of *Pinus* have been identified from the Nut Beds, the genus is represented by wood fragments, dispersed pollen, and by a pollen cone. The pollen cone, described above, is known from a single specimen preserved in siltstone from the upper part of Face 1 of the Nut Beds (Pl. 1, fig. 6). Sectioned longitudinally (Pl. 1, figs. 7–9), the specimen shows the arrangement of microsporophylls typical of Pinaceae. The pollen itself is poorly preserved, possibly immature. Similar pollen cones (Pl. 1, fig. 3), preserved as compressions, occur in association with foliage of a 5-needle pine and seeds of the articulate type (Pl. 1, figs. 4, 5) at the West Branch Creek locality of the Clarno Formation. Although the single specimen from the Nut Beds is broken so that the full length cannot be determined, comparison with the West Branch Creek specimens indicates a length of about 4 cm. Abraded pinaceous seed cones also occur in the Nut Beds (e.g., Pl. 1, fig. 2), but because of poor preservation, they have not been identified to genus.

Family **TAXACEAE** Gray

The Taxaceae, or yew family, has five extant genera and about 20 species of trees and shrubs (Price, 1989). Although the family is well documented by foliage of various genera in the Tertiary of Europe and North America, reports based on seeds are rare. Three genera of taxaceous seeds occur in the Nut Beds: *Taxus*, *Torreya*, and a new extinct genus, *Diploporus*. A single taxaceous leaf, with cuticle corresponding to that of *Torreya*, was recovered from the White Cliffs locality of the Clarno Formation. The leaf is noteworthy for its large size: 70 mm long, 7 mm wide.

Genus **TAXUS** L.

Taxus masonii sp. nov.

Plate 2, figures 1–11

Etymology.—This species is named for Herbert L. Mason, in recognition of his pioneering investigations of fossil conifers from western North America.

Description.—Seed bilaterally symmetrical, lenticular in cross-section, nearly elliptical in face view, base truncate, apex keeled; length 4.3–6.2, avg. 5.3 mm (SD=0.53, n=10), width across plane of symmetry 4.5–5.6, avg. 4.9 mm (SD=0.34, n=10), thickness 3.3–4.0, avg. 3.7 mm (SD=0.28, n=10), length/width ratio 1.0–1.1; basal truncation perpendicular to central axis of seed, elliptical with a pair of small circular vascular scars; apical keel slightly arched as viewed from above, with a central micropylar scar; seed coat about 250–300 μm thick, composed of isodiametric cells 25–60 μm in diameter; two vascular strands, one along each side in the dorsiventral plane, arising from the basal truncation and passing into the seed cavity in the lower ⅓ of the seed.

Specimens.—Holotype: USNM 355474. Paratypes: UCMP 10622, UF 6643, 6644, 9474–9478, 9801, 9802, USNM 354997, 354998, 355000, 355406.

Discussion.—*Taxus* is represented by permineralized seeds from the Nut Beds that are readily recognized by their lensoid cross section, keeled apex and truncate base (Pl. 2, figs. 1–8). The pointed end represents the micropyle, and the basal truncation corresponds to attachment of the aril with the seed. The pair of vascular scars on the basal truncation (Pl. 2, figs. 7, 8) are diagnostic for the genus. Although extant *Taxus* seeds may vary from two- to three-fold symmetry, these fossil seeds are nearly all bilaterally symmetrical. The morphology and vascular supply of the seed, as seen in serial transverse sections (Pl. 2, figs. 9–11), is very similar to that observed in extant species (Dupler, 1920).

Taxus grows today in central Malesia and Mexico as well as in north temperate areas. The genus has also been confirmed from the Oligocene and Miocene of eastern Europe through careful study of cuticularly preserved leaves (Kvaček, 1982).

Genus **TORREYA** Arn.

Torreya clarnensis sp. nov.

Plate 2, figures 12–16; Text-figure 8A

Etymology.—The epithet clarnensis refers to the Clarno Formation, source of the specimens.

Description.—Seed bilaterally symmetrical, obovate in face view, fusiform in lateral view, elliptical in transverse section; length 19.5–20.8 mm, width 10.7–11.3 mm, thickness across the dorsiventral plane 9.5–9.6 mm, length/width ratio 1.7–1.9; base acute-rounded, apex rounded in face view, acute in lateral view, with the dorsal and ventral faces meeting to form a keel in the apical ⅓ of the seed; micropylar scar at the midpoint of the apical crest; two circular vascular scars situated in the dorsiventral plane, one on either side of the seed; the vascular scars positioned at the level of greatest seed width, about ⅓ of the length from the apex.

Specimens.—Holotype: UF 6510. Paratypes: USNM 353966, 422380.

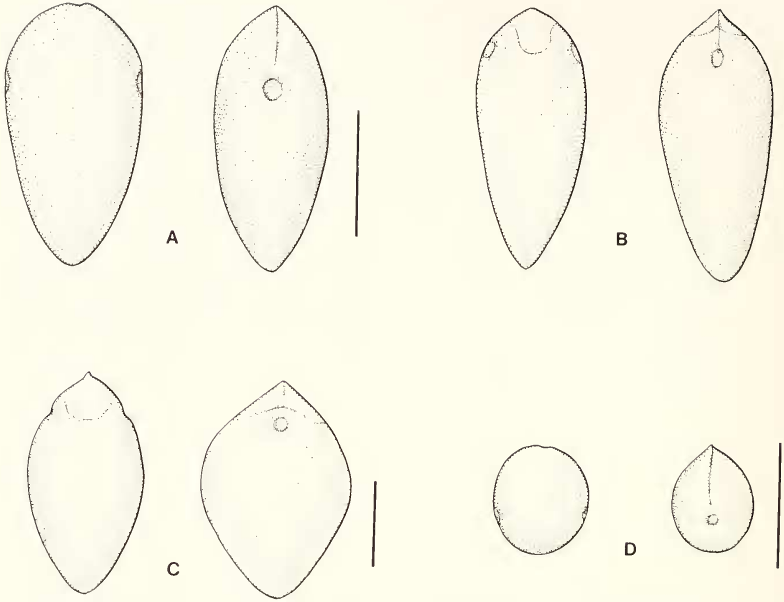
Discussion.—*Torreya clarnensis* is represented only by a few specimens but they present enough characters to establish firmly the affinities with extant *Torreya*. The apical keel, the pair of pores (vascular scars) piercing the seed coat near the apex in the dorsiventral plane (Pl. 2, fig. 13), and the narrowed, acute-rounded base are characters diagnostic of the extant genus. The pair of vascular pores are closer to the apex (Text-fig. 8A) than they are in *Diploporus* (Text-fig. 8D), but not as close to the apex as in the extant species of *Torreya* (Text-figs. 8B, C).

Torreya is a genus of trees with five extant species distributed in North America and eastern Asia. The North American species are restricted to a few sites in California and northwestern Florida. The Asian species are limited to an east–west belt extending from Honshu over the Yang-tse valley to eastern Burma. The genus has also been recognized on the basis of upon fossil foliage from the Late Eocene Florissant and Oligocene Bridge Creek floras (MacGinitie, 1953), and from Oligocene and Miocene localities Europe (Kvaček, 1982).

Genus **Diploporus** gen. nov.

Etymology.—*Diplo* (Gr = twofold) + *poros* (Gr = hole, passage) referring to the pair of vascular scars in the seed coat.

Generic diagnosis.—Seed subovoid, base rounded, apex wedge-shaped; apical keel slightly arched as viewed from above, with a central micropylar scar; seed coat



Text-figure 8.—Seeds of Taxaceae in face view and lateral view, showing apical keel and variable position of the pair of vascular pores in the seed coat. **A**, *Torreya clarnensis* sp. nov., with pores positioned about ⅓ of seed length below apex. **B**, *T. grandis* Fort. from Kuling, China, showing pointed base, apical pores. **C**, *T. taxifolia* Arn. from northwestern Florida showing apical pores. **D**, *Diploporus torreyoides* sp. nov., showing apical keel, pair of pores in the lower half, rounded base. Scale bar = 1 cm.

pierced by a pair of circular vascular scars, one on each side in the dorsiventral plane at, or slightly below, the equator.

Type species.—*Diploporus torreyoides* sp. nov.

Diploporus torreyoides sp. nov.

Plate 3, figures 1–16; Text-figure 8D

Etymology.—The epithet refers to similarity with seeds of extant *Torreya*.

Description.—Seed bilaterally symmetrical, subovoid, ovate to circular in face view, pyriform in lateral view, wide-elliptical in transverse section; length 6.7–8.0, avg. 7.9 mm (SD=0.5, n=25), width 5.4–8.0, avg. 6.9 mm (SD=0.6, n=25), thickness 3.6–7.0, avg. 5.8 mm (SD=0.78, n=25), length/width ratio 1.0–1.3; base rounded; apex rounded in face view, angled in lateral view, with the dorsal and ventral faces meeting to form a sharp crest in the apical ⅓ of the seed with a central micropylar scar; two circular vascular pores situated in the dorsiventral plane, one on either side of the seed, positioned at the level of greatest seed width, about ½ to ⅔ of the length from the apex; aril preserved in some specimens, completely covering seed, 1.0–1.5 mm thick, outer surface of aril with numerous short longitudinal grooves; seed coat smooth; embryo straight, 1.0 mm in diameter, 6.4 mm long, aligned with the central axis of the seed.

Specimens.—Holotype: UF 8542. Paratypes: UF 8501–8541, USNM 355072 (2 specimens), 355471, 355479, 355481 (9 specimens), 355489 (17 specimens), 424744, 424745, 435098, OMSI Pb217, Pb1348, internal casts; UF 6531, 9587, 9803, 9804, USNM 355569, 446078, specimens with intact seed coat and aril.

Discussion.—Represented by more than 75 specimens, this species is among the more common fossils from the Nut Beds, and is particularly abundant near the top of Face 3. Most specimens are smooth-surfaced, representing internal molds of the seed coat (Pl. 3, figs. 9–12); a few possess an additional outer layer about one mm thick with a wrinkly external surface (Pl. 3, figs. 1–8). This outer layer is poorly preserved anatomically but apparently represents the aril. Salient features of these fossils are the rounded base, keeled apex and the pair of conspicuous pores, one on either side in the dorsiventral plane (Pl. 3, figs. 6, 8, 11–13). Longitudinal and transverse sections reveal a slender cylindrical embryo (Pl. 3, figs. 14–16) that is medial within the seed.

Diploporus is interpreted as an extinct genus of Taxaceae based upon several important similarities with *Taxus* and *Torreya*, including the pair of vascular bundles, the central linear embryo and the apical keel that is slightly arched as viewed from above, with a central micropylar scar. The seed base is rounded, however—not truncate as in *Taxus*, and not pointed as in *Torreya*. The tissue surrounding the embryo within the seed cavity is cellularly preserved in many of the specimens, and has a speckled appearance (Pl. 3, figs. 14–16) like that of *Torreya. Diploporus* seeds are larger than those of *Taxus* and smaller than those of *Torreya*. The pair of vascular pores in the dorsiventral plane corresponds to those seen in *Torreya*, but in the fossil these scars are positioned at or slightly below the equator, rather than near the apex (Text-fig. 8).

Seeds of this morphology have not, to my knowledge, been described from the Tertiary before, and it is of some interest to confirm the presence of extinct Taxaceae surviving into the Tertiary. As this manuscript was going to press, I noticed an apparent close similarity of this genus to the Cretaceous genus *Vesquia* Bertrand from the Wealden Formation of Belgium (Alvin, 1960). Although I have not seen specimens of *Vesquia*, the genus was described in good detail and illustrated with line drawings (on the basis of two well preserved liginfied seeds) by Alvin (1960). *Vesquia* seeds are similar in size and shape to those *Diploporus*, with a corresponding pair of pores ("two formamina") in the lower half. However, the specimens of *Vesquia* are more globose and appear to lack an apical crest. In addition, the basal surface of the *Vesquia* seeds have a pair of grooves leading to the foramina, which are not seen in *Diploporus. Vesquia* is also considered to belong to the Taxaceae and, among extant genera, compares most closely to *Torreya* (Alvin, 1960). It is possible that additional work may reveal that the Clarno taxon is a hold-over from the Mesozoic. Indeed, both of the living genera, *Torreya* and *Taxus*, are believed to extend back to the Jurassic (Florin, 1958; Harris 1976).

Family **ACTINIDIACEAE** Hutch.

This family includes four modern genera: *Clematoclethra*, *Sladenia*, *Saurauria* and *Actinidia*. The latter, which provides the kiwi fruit of commerce, is the best known. *Saurauria* has been reported on the basis of leaves from the middle Eocene of Alaska (Wolfe, 1977) and Wyoming (MacGinitie, 1974). Seeds assigned to the fossil genus *Pasternackia* (described, p. 104) are similar to those of *Saurauria*, although affinities remain uncertain. The following constitutes the first recognition of *Actinidia* from the North American fossil record.

Genus **ACTINIDIA** Lindl.

Actinidia oregonensis sp. nov.

Plate 4, figures 1–4

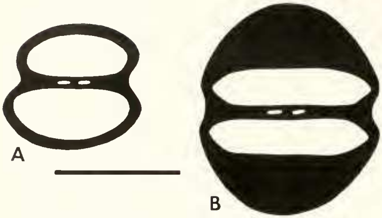
Etymology.—The epithet refers to the state of Oregon.

Description.—Seed bilaterally symmetrical, anatropous, elongate-elliptic in face view, laterally flattened, keeled in the plane of symmetry, lensoid in cross section; length 3.2–4.4, avg. 3.8 mm (SD=0.46, n=5), width 2.2–3.0, avg. 2.5 mm (SD=0.29, n=7), thickness 1.0–1.1, avg. 1.1 mm (SD=0.05, n=7); base with obtusely pointed micropyle and laterally adjacent hilum, apex rounded; seed coat ca. 0.1 mm thick, surface reticulate, made up of thick-walled, polygonal (five- to seven-sided), isodiametric cells 190 to 240 μm decreasing in size toward the raphe and antiraphal edges of the seed; 15–20 cells wide in face view.

Specimens.—Holotype: UF 6292. Paratypes: UF 6293, 6294, 6498, 8580, 9218, USNM 355370.

Discussion.—This species is represented by chalcedony seed casts. The distinctive reticulate surface of these fossil seeds (Pl. 4, figs. 1–4) matches that in extant *Actinidia* seeds, where the outer layer of the seed coat is formed by polygonal cells with strongly thickened lateral walls. This surface ornamentation, combined with seed shape, and position of the hilum and micropyle, confirms the identification of these fossils as *Actinidia*.

Actinidia is a genus of about 30 species of climbers distributed in Indomalesia and eastern Asia. Although this is the first report of fossil *Actinidia* from North



Text-figure 9.—Transverse sections of *Alangium* endocarps from the Nut Beds. **A**, *A. eydei* sp. nov., showing relatively thin endocarp wall, and one locule somewhat larger than the other. **B**, *A. rotundicarpum* sp. nov., showing thick walls, and locules equal in size.

America, seeds of the genus occur from the upper Oligocene to Pliocene of Europe (Kirchheimer, 1957; Dorofeev, 1963; Mai and Walther, 1978; Friis, 1985).

Actinidia oregonensis seeds are large in comparison to the four extant species that I have seen (*A. arguta* Franch. et Sav., *A. callosa* Lindl., *A. chinensis* Planch., *A. strigosa* Hook. f. et Thoms.). Whereas the fossils average about 4 mm in length, the extant species examined, and most of the European fossil specimens, are about 2 mm long. *Actinidia* seeds from the Pliocene of the Netherlands, however, range from 1.8 to 4 mm long (Kirchheimer, 1957). Kirchheimer (1957) placed all of the European specimens in a single fossil species, *A. foveolata* Reid and Reid, but Friis (1985) stated that the type material of *A. foveolata* is larger than the Danish and Polish material and has a greater number of cell rows across the width of the seed.

Family ALANGIACEAE DC.

The Alangiaceae are a tropical family with one genus and about 20 living species in Africa and from China to Australia. *Alangium* grows as a tree, less often as shrubs or lianas. The genus has an excellent fossil record in Europe and North America (Eyde, Bartlett and Barghoorn, 1969; Mai, 1970). Although allied to the Cornaceae, and placed in the Cornales by Cronquist (1981), *Alangium* differs by the presence of laticifers and alkaloids (Eyde, 1988). The genus is divided into four sections that are distinguished on the basis of style, stigma, stamen, floral vascular system and endocarp characters (Eyde, 1968). The paleogeographic history of *Alangium* is reviewed by Krützsch (1989).

The Nut Beds flora includes two species of *Alangium* based upon fruits. Silicified wood of this genus is also known from the Nut Beds (Scott and Wheeler, 1982). Based upon the presence of scalariform perforation plates, small intervascular pits and long vessel elements, Scott and Wheeler (1982) determined that *Alangium oregonensis* wood conforms to Metcalfe and Chalk's (1950) "group A" (*A. javanicum* type), and differs from "group B" (*A. chinense* type). This observation is of interest because the fruit morphology of the species considered below corresponds closely to that of extant *A. chinense* Rehder.

Genus ALANGIUM Lam.

Alangium eydei sp. nov.

Plate 4, figures 5–14, Text-figure 9A

Etymology.—This species is named for the late Richard Eyde, in recognition of his contributions in understanding the morphology of living and fossil *Alangium* and other Cornales.

Description.—Endocarp bilocular, ovate in face view, laterally compressed in the plane of septum; base rounded, apex obtuse-pointed; length 4.9–10.3, avg. 7.7 mm (SD=1.7, n=13), width 5.1–7.6, avg. 6.3 mm (SD=0.75, n=11), thickness 3.2–6.4, avg. 4.3 mm (SD=0.75, n=15); one locule slightly smaller than the other; each locule with a single seed; endocarp surface relatively smooth with faint broad ridges; position of the septum marked on the exterior of the endocarp by a peripheral furrow between the two carpels; septum ca. 0.4 mm thick, containing six to eight canals that radiate in the median plane and terminate before reaching the edge of the endocarp, forming an asterisk pattern; endocarp wall ca. 0.5 mm thick, made up of isodiametric polygonal sclereids 17–30 μm; locule lining uniseriate, 17.5 μm thick, composed of cuboidal sclereids.

Specimens.—Holotype: USNM 424646, endocarp. Paratypes: HU 60003, 60004, UCMP 10710, UF 6311, 6508, 6645, 6646, USNM 354012–354015, 354016 (2 specimens), 354018, 354019, 354045, 422393, 424645, 446073, endocarps; UF 9479, USNM 354020, septal canal casts; USNM 354017 (20 specimens), isolated locule casts.

Discussion.—*Alangium eydei* is represented in the Nut Beds by occasional endocarp casts (Pl. 4, figs. 5–8) and permineralizations (Pl. 4, figs. 11–12). The latter may be sectioned to reveal internal morphology and anatomy (Pl. 4, fig. 13). Frequently all that remains of the endocarp is a carbonaceous powder that disintegrates in the field, leaving the two chalcedony locule casts side by side, resembling a sandwich (Pl. 4, figs. 9, 10). Sometimes star-shaped chalcedony casts of the canals within the septum are recovered (Pl. 4, fig. 14) but the most common remains of *Alangium* in the Nut

Beds collections are isolated silica locule casts, preserved as thin, elliptical wafers with a faint stellate impression on one side corresponding to the septal canals.

This species, like most of those known from the Tertiary (Eyde, Bartlett and Barghoorn, 1969; Mai 1970), corresponds to section *Marlea* of extant *Alangium* in having a bilocular, thick-walled endocarp. Eyde (1968) noted that the extant species of this section can be arranged in a sequence to show the gradual loss of one of the carpels. In *Alangium kurzii* Craib the locules are more or less equal in size, whereas in *A. platanifolium* (S. et Z.) Harms, *A. alpinum* W. Smith et Cave and *A. rotundifolium* (Hassk.) Bloemb. one of the carpels is much smaller than the other, often with a tightly closed abortive locule, and in *A. griffithii*, only one carpel is evident. The fossil closely resembles *A. chinense* Rehder in having one locule smaller than the other (Text-fig. 9A), but with both locules fertile. Eyde (1968, fig. 3h) illustrated a transverse section of an endocarp of extant *A. chinense* that is almost identical to that seen *A. eydei* (Pl. 4, fig. 13). The smaller of the two carpels generally is at least 80% of the size of the larger carpel both in the fossil and in *A. chinense*.

Alangium eydei bears a close resemblance to *A. jenkensii* Chandler (1961b) from the London Clay, although the largest of the Nut Beds specimens is slightly smaller than the single London Clay specimen. Although *A. jenkinsii* clearly belongs to *Alangium*, Chandler (1961b) noted that "owing to the poor condition of the single specimen it is difficult to define specifically." *A. vermontanum* Eyde et Barghoorn from the Oligocene Brandon Lignite of Vermont (Eyde, Bartlett and Barghoorn, 1969) differs from *A. eydei* in having a much more reduced smaller locule, and in the reticulate sculpture of the ventral side of the larger locule. The Clarno fossil differs from *A. dubium* (Unger) Mai from the Miocene of central Europe (Mai, 1970, p. 474) in the lack of transverse ridges on the endocarp surface.

Alangium rotundicarpum sp. nov.

Plate 4, figures 15, 16, Text-figure 9B

Etymology.—*Rotundus* (L = circular, round), + *karpos* (Gr = fruit), referring to the rounded outline resulting from thick wall of the endocarp.

Description.—Endocarp subglobose, bilocular; length 8.5 mm, width 7.2 mm, thickness 7.7 mm; locules approximately equal in size, each with a single seed; position of the septum marked at the endocarp surface by a peripheral furrow between the two carpels; septum 0.5 mm thick, containing six to eight canals that radiate in the median plane and terminate before reaching the edge of the endocarp, forming an asterisk pattern; endocarp wall 2.75 mm thick dorsally and ventrally, thinner laterally, made up of isodiametric to anticlinally elongate sclereids, 40–150 μm in diameter; locule lining not well preserved, 30 μm thick.

Specimen.—Holotype: USNM 435005.

Discussion.—This species, known from a single permineralized specimen, differs from *A. eydei* in its globose endocarp (Pl. 4, fig. 15) with thick lateral walls and in the equivalent size of the two locules (Text-fig. 9B). Although the exterior surface of the endocarp is not preserved, the intact portion is about five times thicker than the complete wall of *A. eydei*. Transverse sectioning revealed that the locules of *A. rotundicarpum* are approximately equal in size (Pl. 4, fig. 16), in contrast with the unequal development of locules in *A. eydei* (Pl. 4, fig. 13). The endocarp includes anticlinally elongate sclereids, whereas those of *A. eydei* are more or less isodiametric. In size of the endocarp and unusually thick endocarp wall, this species resembles *A. krutzschii* Mai from the middle Eocene Geiseltal flora of Germany (Mai, 1970); the locules of that species, however, are much smaller.

Family **ANACARDIACEAE** Lindley

The Anacardiaceae, or sumac family, includes about 70 extant genera of tropical to temperate distribution including trees, shrubs and lianas, and is divided into five tribes: Anacardieae (eight genera), Spondiadeae (17 genera), Rhoeae (40 genera), Semecarpeae (five genera), Dobineeae (one genus). The Spondiadeae, characterized by drupes with hard, often multilocular, stones having oval germination apertures, is well represented in the fossil record, with records of both extant and extinct genera in the early Tertiary of Europe (Reid and Chandler, 1933; Collinson, 1983) and North America.

The Anacardiaceae are represented in the Nut Beds flora by at least two genera of fruits: *Rhus*, of the tribe Rhoeae, and the extinct genus *Pentoperculum* of the tribe Spondiadeae. In addition, the fruit described herein as *Pistachioides* (p. 105) resembles that of extant *Pistachia*, and might also belong to the Anacardiaceae. Anacardiaceous woods from the Nut Beds include *Tapirira* (tribe Spondiadeae; Manchester, 1977), and at least one additional genus remaining to be described (S. R. Manchester, unpublished).

Genus **PENTOPERCULUM** gen. nov.

Etymology.—*Penta* (Gr = five) + *operculum* (L = lid), referring to the five germination valves of the fruit.

Type species.—*Pentoperculum minimus* (Reid et Chandler), comb. nov.

Pentoperculum minimus (Reid et Chandler) comb. nov.

Plate 5 figures 1–17

Dracontomelon minimus Reid et Chandler 1933, p. 302, pl. 13, figs. 20–24.

Description.—Endocarp subglobose to more or less oblate, five-(rarely four- or six-) carpellate, roundly pentangular (rarely quadrangular or hexagonal) in transverse section, length 4.4–6.5, avg. 5.7 mm (SD=0.49, n=23), equatorial diameter 4.5–8.5, avg. 6.8 mm (SD=0.89, n=24), length/equatorial diameter ratio 0.74–1.11, avg. 0.90, widest at the equator; base round to flat with a slight depression ca. 1 mm in diameter at the extreme base, apex rounded; locules five (rarely four or six), single-seeded, radially arranged, vertically elongate, 3.5–5.0 mm long, 1.5–2.1 mm wide, 2.1–3.3 mm in dorsiventral dimension; each locule with a convex, dorsal-apical, germination valve, resulting in five (rarely four or six) elliptical bulges at the surface of the endocarp extending from the equator almost to the apex; germination valves 440 μm thick, two-partite with a median longitudinal slit of shutter-like splitting; lacunae alternating with the locules at the equator of the fruit corresponding in position to the exterior angles of the fruit; these lacunae about as wide as the locules, but shorter both dorsiventrally and axially; central axis of the fruit with a cylinder of vascular tissue extending from base spreading and dissipating apically; endocarp wall and septa composed of isodiametric sclereids 28–45 μm in diameter with interspersed tracts of fibers; locule lining 25–30 μm thick, composed of horizontally aligned fibers, these fibers 7 μm in diameter and at least 10 μm long.

Specimens.—UCMP 10633, UF 5708–5711, 6608–6610, 10634, UM 31604, USNM 312762 (Bones, 1979, pl. 3, fig. 6), 353967 (10 specimens), 353969, 422390, 424851, 435106–435114, endocarps; UCMP 10635–10637, UF 6664–6671, 9317, 9736 (100 specimens), USNM 435115 (7 specimens), isolated locule casts. Holotype: BM v22546 from the London Clay.

Discussion.—Specimens of *Pentoperculum* are preserved in the Nut Beds as white chalcedony casts of the endocarp and as permineralized endocarps with intact seeds. Most specimens are pentalocular (e.g., Pl. 5, figs. 1, 2, 8), although two specimens are four-loculed (e.g., Pl. 5, fig. 15) and three are six-loculed (USNM 435107–435109). In some cases the endocarp has disintegrated leaving a cavity in the matrix with protruding chalcedony locule casts. Isolated locule casts are common (Pl. 5, figs. 5, 6). Because the fossil does not correspond precisely to any living genus, the new generic name *Pentoperculum* is established to accommodate this species. *Pentoperculum minimus* was a widespread species that occurred in the Eocene of Hungary (Kovacs, 1957), as well as England (Reid and Chandler, 1933) and western North America.

This species was first recognized on the basis of pyritized endocarps and locule casts from the London Clay flora (Reid and Chandler, 1933), an example of which is included in Pl. 5, fig. 14. The Nut Beds specimens are indistinguishable both in external and internal morphology from the type material. Reid and Chandler (1933) demonstrated similarities to the extant genus *Dracontomelon*, and their work confirmed affinities with the tribe Spondiadeae. However, new observations based upon sections of the fossil and extant endocarps indicate significant differences between *Pentoperculum* and *Dracontomelon*. Contrary to the interpretation of Reid and Chandler (1933), serial sections (e.g., Pl. 5, figs. 9, 10) indicated that the lacunae are not linked to peripheral apertures in the fossil, a condition considered diagnostic of the extant genus. The fossil fruits are more symmetrical than those of *Dracontomelon*, with more or less equal development of locules. In addition, the fossil endocarps are much smaller than those of the living species of *Dracontomelon*. In contrast to *Dracontomelon*, in which each of the locules opens by the "uncorking" of an undivided apical plug (Hill, 1933), the locules of *Pentoperculum* open by means of a bipartite operculum (Pl. 5, fig. 8).

Various modes of germination occur in the fruits of the Spondieae and are described in detail by Hill (1933, 1937). The apertures of *Pentoperculum* appear to have had shutter-like valves similar to those observed in *Haematostaphis* (Hill, 1933) and *Pseudospondias* (Hill, 1937). In these genera, "the lid separates into two equal halves which are pushed apart and thrown aside by the radicle as it emerges" (Hill, 1933, pp. 881–882).

Genus **RHUS** L.

Rhus rooseae sp. nov.

Plate 6, figures 1–8

Etymology.—This species is named after Carrie L. Roose, recognizing her helpful assistance and support of this project.

Description.—Fruit bilaterally symmetrical, subelliptic, unilocular, laterally flattened in the plane of symmetry, transversely elliptic in cross section, base and apex obtuse-rounded; width greater than height; height 3.3–4.3, avg. 3.8 mm (SD=0.29, n=8), width 4.2–5.1, avg. 4.7 mm (SD=0.4, n=5), thickness 1.5–2.0, avg. 1.8 mm (SD=0.25, n=9); mesocarp with 25–30 prominent longitudinal vascular bundles; endocarp surface smooth, shiny, with a circular funicular depression in the plane of symmetry, and a slight bulge on the opposite side; endocarp wall 400 μm thick, composed of three layers: inner layer 250 μm thick, uniseriate, composed of anticlinally oriented columnar cells 250 μm high and 20–30 μm wide; the next layer much thinner, also uniseriate, 33 μm thick, composed of rectangular cells typically 45 μm wide; the overlying layer uniseriate, composed of columnar cells similar to the first, but only 80 μm thick, capped by a uniseriate to triseriate layer of rectangular cells.

Specimens.—Holotype: USNM 355036. Paratypes: UF 9350–9352, 9417–9422.

Discussion.—Sumac fruits, *Rhus rooseae*, typically are preserved in the Nut Beds as translucent, silicified endocarps. The prominent columnar cell construction is exhibited both in fractured specimens by SEM (Pl. 6, figs. 5, 6) and with transmitted light in thin sections (Pl. 6, fig. 8). Only one specimen, designated the holotype, has the mesocarp intact showing the prominent longitudinal vascular bundles (Pl. 6, figs. 1–3).

Fruit and seed morphology of *Rhus* are reviewed by von Teichman and Robbertse (1986). *R. rooseae* shares many characters with extant *Rhus* including lateral compression in the plane of bisymmetry, width greater than height, longitudinal vascular bundles forming ribs in the mesocarp, and endocarp comprised of two or more layers of anticlinally elongate columnar cells. Although *Rhus* has been reported commonly on the basis of leaves from the North American Tertiary, this is the first North American report based upon fruits. The genus has also been documented on the basis of fruits similar to extant *Rhus toxicodendron* L. from the Middle Miocene of Denmark (Friis, 1979). The Danish fossil differs from *R. rooseae* in possessing only about 12, rather than 25–30, longitudinal ribs.

Family **ANNONACEAE** Juss.

The Annonaceae are a family of trees, shrubs and lianas with about 128 living genera and 2050 species. The family is mostly tropical, with the exception of few genera that extend into temperate regions. Three species of Annonaceae can be identified from the Nut Beds on the basis of internal molds of the seed coat, showing the characteristic ruminate endosperm.

Genus **ANONASPERMUM** Ball emend. Reid et Chandler

Reid and Chandler (1933) emended the fossil genus *Anonaspermum* Ball to accommodate anatropous seeds with ruminate endosperm of the various types found in the family Annonaceae, and with an encircling band of fibers formed by the raphe and chalaza, which divides the seed into more or less symmetrical halves, with the hilum terminal. Most of the fossils that have been attributed to this genus are internal molds of the seed coat, or endosperm casts, with the seed coat missing. Distinctive surface patterns result from the configuration of the ruminate endosperm.

The Clarno specimens of *Anonaspermum* have been segregated into three species using criteria similar to those used in distinguishing London Clay species. Fourteen species of *Anonaspermum* were described from the London Clay (Reid and Chandler, 1933; Chandler, 1961b; summarized, Collinson, 1983), based upon differences in seed shape, pattern of ridges in endosperm, and nature of the encircling fiber band. As noted by Collinson (1983, pp. 73–74), "Many different fossil forms may be recognized but it is very difficult to relate these to living genera. Similar endosperm patterns may occur in different living genera and different endosperm patterns may occur within the same living genus". It is possible that the three Nut Beds species recognized here were actually produced by different genera, but because of the limited systematic resolution provided by seed characters in this family, they are all be placed in the stereotypic genus *Anonaspermum*.

Anonaspermum cf. **pulchrum** Reid et Chandler
Plate 6, figures 9–15

Description.—Seed bilaterally symmetrical, short- to long-ellipsoid, all faces convex rounded, sometimes slightly flattened laterally in the plane of symmetry; length 5.5–10.3, avg. 8.0 mm (SD=1.47, n=10), width 3.8–6.2, avg. 5.2 mm (SD=0.85, n=12), thickness 3.4–4.9, avg. 4.3 mm (SD=0.42, n=12); without a marked longitudinal median depression; internal mold of seed coat with rumination ridges many, narrow, transverse, interrupted in course; these ridges mainly continuous across the center, without forming pits, nodules or punctae; sometimes with short grooves along the ridge crests; ruminations tetrapartite in transverse section; with a strap-like ridge 1–1.4 mm wide in the plane of symmetry formed by fibers of the raphe and chalaza; hilum terminal at the broader end of the raphe ridge; seed coat thin (80–100 μm), smooth.

Specimens.—HU 60061, UCMP 10676, 10677, UF 5233, 5234, 6574, USNM 353971 (7 specimens), 353972, 353975, 353976, 424794–424797, 434983.

Discussion.—This species is represented in the Nut Beds mostly by internal molds of the seed coat (i.e., endosperm casts). In one specimen (UCMP 10677) part of the thin seed coat is adhering. In seed shape, size and pattern of endosperm ruminations, this species corresponds closely to *Anonaspermum pulchrum* Reid et Chandler from the London Clay flora. Reid and Chandler (1933) described the raphe and chalaza as lying in a rather inconspicuous marginal groove, but in most of the Clarno specimens these form a ridge (Pl. 6, figs. 10, 13). Perhaps this difference is due to abrasion of the London Clay specimens resulting in loss of the fibrous band. In some of the Nut Beds specimens, the fibrous band is partially or entirely broken away (e.g., Pl. 6, fig. 15) revealing a marginal groove like that of the London Clay species. Reid and Chandler (1933) called attention to similarity with the living Indomalaysian species *Dasymaschalon clusiflorum* Merrill, but refrained from suggesting a close relationship because of the likelihood that similar seeds could be found elsewhere in the family with a more exhaustive search of modern genera.

Anonaspermum bonesii sp. nov.
Plate 6, figures 16–18

Etymology.—This species is named for the late Thomas J. Bones, who collected most of the *Anonaspermum* specimens known from the Nut Beds.

Description.—Seed roughly ellipsoidal, pointed apically, with a slight flattening near the hilum, rounded basally, bilaterally symmetrical, laterally compressed in the plane of symmetry such that the thickness is less than ⅓ of the width, with some shallow depressions on the flattened face; length 11.7 mm, width 7.4 mm, thickness 2.5 mm; internal mold of seed coat with ruminations transverse in the midsection of seed, but radially oriented near the base and apex, thin, closely spaced, irregular, disappearing toward the center of the face, giving rise to fine punctae; inner layer of seed coat with a criss-cross pattern of straight to somewhat curved fibers.

Specimen.—Holotype: USNM 353975.

Discussion.—This species, known from a single silicified seed, differs from *A.* cf. *pulchrum* in its pronounced lateral compression (Pl. 6, fig. 18), such that the thickness is less than ⅓ of the width, and by the orientation of ruminations. Although the ruminations are transversely oriented across most of the seed in *A.* cf. *pulchrum* (Pl. 6, figs. 9, 10, 14), they are radially oriented in the apical and basal ⅓ of the *A. bonesii* seed (Pl. 6, figs. 15, 17).

Anonaspermum rotundum sp. nov.
Plate 7, figures 1, 2

Etymology.—*Rotundus* (L = circular, round) referring to the seed shape.

Description.—Seed wide-ellipsoidal, rounded apically and basally, laterally compressed in plane of the raphe; length 13.5 mm, width 12.0 mm, thickness 6.0 mm; internal mold of seed coat with ruminations radially oriented from the center, thin, short, irregular, shorter toward the center; raphe band extending nearly 350° around periphery of the seed.

Specimen.—Holotype: USNM 435099.

Discussion.—*A. rotundatum* is known from a single specimen which is preserved as an internal mold of the seed coat. The specimen differs from those of the other two Clarno species by its larger size and nearly circular outline.

Family **ARALIACEAE** Juss.

The Araliaceae, as traditionally circumscribed, are a family of about 57 genera and 800 species including trees, shrubs and lianas mostly of tropical distribution. The more cosmopolitan, mostly herbaceous Apiaceae (Umbeliferae) with 418 genera and 3100 species, are very similar and should be included within Araliaceae to have a monophyletic family (W. Judd, pers. comm., 1991; and see Mabberley, 1989).

Genus **PALEOPANAX** gen. nov.

Etymology.—*Paleo* (Gr = old) + *panax* (L, Gr = ginseng) referring to the ginseng family, Araliaceae.

Type species.—*Paleopanax oregonensis* sp. nov.

Paleopanax oregonensis sp. nov.
Plate 7, figures 3–4

Description.—Fruit wide-elliptical in face view, bicarpellate, bilaterally symmetrical, dorsiventrally compressed, with an epigynous perianth bulge; base flat or somewhat cordate, apex rounded; length 4.5–5.6 mm, width 5.4–6.6 mm, estimated thickness 1–2 mm; carpels D-shaped in face view, with two to three arched longitudinal grooves, adjoined ventrally at the central fruit axis by their straight margins, outer margins convex, smooth; pedicel >2.0 mm long, >0.3 mm thick; two styles arising parallel to each other from the apex, 2.0–3.0 mm long, recurving distally.

Specimens.—Holotype: OMSI Pb810. Paratypes: OMSI Pb1779, Pb1014.

Discussion.—This species, represented only by compression fossils, was recovered from the leaf horizon at the base of Face 3 in the Nut Beds. The preservation of the styles indicates that they were tough and persistent, or that the fruits were deposited without rigorous transport.

Fruits of *Paleopanax* conform to those of the Apiales (Araliaceae + Apiaceae) in the possession of epigynous perianth, styles as many as the carpels and schizocarp morphology. Although samaroid schizocarps also occur in Sapindaceae and Aceraceae, the epigynous tepals rule out these families. In addition the apical bulge in the perianth region (Pl. 7, fig. 3) may be interpreted as a nectary disk, as is characteristic of Apiales. Paired thin mericarps are characteristic of Apicaceae and also occur in some Araliaceae. Specialized carpophores of the type found in Apiaceae do not appear to be developed in this fossil.

Similar fruits occur in the extant genus *Pseudopan-*

ax. Fruits of *P. davidii* (Franch.) W.R. Philipson from western Hupeh, China (Pl. 7, fig. 5) are particularly similar to the fossil. However, *Pseudopanax* has a single style that divides distally into two arms, whereas the fossil has two distinct styles.

Family **BETULACEAE** Gray

The Betulaceae are a family of six extant genera, with an excellent fossil record in the northern hemisphere (Crane, 1989). The family is represented in the Nut Beds by the two fruit types described below, *Coryloides* and *Kardiasperma*, and by wood attributed to *Betula* (Scott and Wheeler, 1982). The family is represented at other Clarno Formation localities, including West Branch Creek and White Cliffs, by leaves and infructescences of *Alnus* and by fruits that may be similar to *Palaeocarpinus*. Also a fruit resembling a small shuttle-cock, *Calycites ardtunensis* Crane, is known from West Branch Creek, White Cliffs and Gosner Road localities of the Clarno Formation, and may represent an extinct genus of the Betulaceae (Crane, 1989).

Genus **CORYLOIDES** gen. nov.

Etymology.—The generic name refers to the similarity of these fossils to nuts of *Corylus*.

Type species.—*Coryloides hancockii* sp. nov.

Coryloides hancockii sp. nov.

Plate 7, figures 6–12, 16–18

Etymology.—The species is named in honor of the late Alonzo W. Hancock, amateur fossil collector and founder of the field station adjacent to the Nut Beds locality.

Description.—Nut nearly perfectly spherical, rounded apically and basally; unilocular, single seeded; outermost surface as seen in casts and external molds strongly ribbed meridionally; ribs spaced 2–4 mm apart at the equator; fruit wall 0.8–1.2 mm thick with a large longitudinal vascular bundle corresponding to each of the external ribs. Nut cast spherical, length 24.8–37.5, avg. 28.8 mm (SD=2.65, n=30), equatorial diameter 23.0–32.6, avg. 27.5 mm (SD=2.48, n=30), with a prominent basal scar about 20–25 mm in diameter and a circular stylar protrusion 1.5–2.5 mm in diameter at the apex; surface of nut cast above the basal scar with faint longitudinal ridges corresponding in position to the ribs on the fruit surface; perimeter of the basal scar forming a circumscissle band ca. 2–3 mm wide with a smooth, circular upper margin at which point the longitudinal surface ribs begin, and a more jagged lower margin with the broken ends of vascular bundles corresponding to the surface ribs, where they may have been torn away from the involucre; nut surface slightly recessed over the basal scar. Seed more or less globose, ca. 20–24 mm in diameter, longitudinally wrinkled, with a large circular hilum, about 9.5 mm in diameter at one end.

Specimens.—Holotype: UF 8497. Paratypes: UF 8492–8496, 8499, 9898, USNM 40544 (Scott, 1954), 354408, 354425, 354620, 354630, 354632, 354634–354636, 354641–354643, 354645, 354647, 354650, 354654, 354658, 354677, 354757, 354811, 354903, 354922, 354984, 354986, 354992, UWBM 35268, 35269, nut casts; UF 8498, nut with seed partially exposed; UM 29942, seed.

Discussion.—*Coryloides* is distinguished by a nearly spherical, meridionally ridged nut with a large circular circumsissle mark on one end (Pl. 7, figs. 7, 8, 9, 10) and a small stylar scar at the other (Pl. 7, figs. 6, 8). The chalcedony-replaced nuts are attractive specimens with the shape and density of a large game marble. The fruits occur mainly at the top of Faces 3 and 4 in the Nut Beds, and are not known from other localities of the Clarno Formation. Although these specimens were informally identified as palm fruits (Gregory, 1969; Bones, 1979), the large circular band at the basal end of the nut is inconsistent with the morphology of extant Palmae. The cellular anatomy of the nutshell usually is not preserved but in one of the more completely preserved, although somewhat crushed, specimens, transverse sectioning reveals the thickness and sculpture of the outer wall, and shows the presence of a large vascular bundle corresponding in position to each of the surface ribs (Pl. 7, figs. 17, 18).

Scott (1954) figured a fruit cast (p. 86, pl. 16, fig. 24) and an isolated seed cast (p. 87, pl. 16, figs. 29, 30) of *Coryloides hancockii* among his incertae sedae. A silicified fruit that has been fractured, revealing an intact seed cast (Pl. 7, fig. 12) provides the basis for linking isolated seed casts, such as that figured by Scott, as belonging to the same species as the fruit casts. The sedimentary mold surrounding the silicified nut cast shows that the external surface was more strongly ribbed (Pl. 7, figs. 11, 16) than the nut cast alone would suggest. The large basal scar indicates probable detachment from an involucre as is seen in the nuts of various Fagaceae and Betulaceae.

The globose form, unilocular, single-seeded structure and prominent basal scar of these nuts at first suggested affinities with cupulate fruits of *Quercus* and *Lithocarpus* in the Fagaceae. Fruits with such prominent longitudinal ridges are not known in the Fagaceae, and the peculiar, more or less crenate pattern of vascular bundles seen on the basal scar is unlike anything observed among extant fagaceous fruits (Kaul, pers. comm., 1989). In addition, the nutshells of *Quercus*, *Lithocarpus* and other Fagaceae do not contain large, widely spaced longitudinal vascular bundles as seen in this fossil.

The affinities of this fruit appear to be close to *Corylus* in the Betulaceae. The nature of the scar left behind on the nut of *Corylus*, where the involucre, or "hull", detaches (Pl. 7, figs. 13, 14), is very similar to that seen in *Coryloides*. This feature, together with the presence of a single locule and seed and the relatively thin nutshell containing unusually large longitudinal vascular bundles (Pl. 7, fig. 15), is consistent with the fossil nuts. However, extant *Corylus* fruits are smaller and not as perfectly globose as those of *Coryloides*. The basal scar of *Coryloides* is nearly circular, whereas that of *Corylus* usually somewhat distorted and elliptical, indicating a difference in the symmetry of involucral attachment. These features, and the prominently ribbed surface of the nuts indicate that the fossils do not belong in the extant genus. Whether *Coryloides* is a sister genus to *Corylus*, or a case of parallel evolution in another line of the Betulaceae is open to speculation.

Genus **KARDIASPERMA** gen. nov.

Etymology.—*Kardia* (Gr = of the heart) + *sperma* (Gr = seed).

Type species.—*Kardiasperma parvum* sp. nov.

Kardiasperma parvum sp. nov.
Plate 8, figures 1–5

Etymology.—*Parvum* (L = little) referring to the small size of the locule casts.

Description.—Locule casts small, dorsiventrally compressed, obcordate, quadrilaterally symmetrical, base rounded or faintly cordate with hilum central, apex blunt-pointed in face view (ca. 90°); length 1.3–2.4, avg. 2.1 mm (SD=0.23, n=19), width 1.0–2.0, avg. 1.7 mm (SD=0.25, n=19), thickness 0.5–1.2, avg. 1.0 mm (SD=0.14, n=19); surface smooth with a keel in the major plane of symmetry and with a median groove running dorsally and ventrally from base to apex in the minor plane of symmetry.

Specimens.—Holotype: USNM 435077. Paratypes: UCMP 10710–10713, UF 6602–6604, USNM 355706–355710, 424705–424710, 424750, 424768, 435076, 435078–435081.

Discussion.—These specimens are morphologically identical to the locule casts of *Palaeocarpinus* from the Paleocene of Almont, North Dakota (Crane et al., 1990, p. 24). There is a marked difference in size, however. Locule casts from the Almont locality are 4–5.5 mm wide, i.e., two to five times larger than the species described above. Although the locule casts of *Kardiasperma parvum* have not been found intact within complete fruits, they correspond in size to fruits of an undescribed species of small, spiny-bracted fruit similar to *Palaeocarpinus* known from compressions (Pl. 8, fig. 20) at the West Branch Creek and White Cliffs localities of the Clarno Formation. *Palaeocarpinus* is an extinct genus of the Coryleae known from the Paleocene of England (Crane, 1981) and North America (Crane et al., 1990; Sun and Stockey, 1992).

Family **BURSERACEAE** Kunth.

The Burseraceae, or torchwood family, comprises 16 genera and about 500 species of tropical trees and shrubs with present centers of diversity in America and northeastern Africa. The family is divided into three tribes (Lam, 1931, 1932; Daly, 1989), based principally upon characters of the fruits. In the tribe Bursereae (*Bursera*, *Commiphora*, *Aucoumea*, *Boswellia*) pyrenes are concrescent but not connate, and have a dry, dehiscent pericarp. In the Protieae (*Protium*, *Garuga*, *Tetragastris*, *Hemicrepidospermum*, *Crepidospermum*) pyrenes are separate and the outer pericarp may be either fleshy or dry and dehiscent. In the Canarieae (*Canarium*, *Scutinanthe*, *Dacryodes*, *Santiria*, *Trattinickia*, *Haplobus*) pyrenes are connate, forming a plurilocular endocarp with a fleshy, rarely more or less dry, indehiscent pericarp. General fruit and seed morphological characters for the family are reviewed by Reid and Chandler (1933, pp. 266–7).

Genus **BURSERICARPUM** Reid et Chandler

Bursericarpum oregonense sp. nov.
Plate 8, figures 6–17

Etymology.—The epithet refers to Oregon, the state in which the Clarno fossils were collected.

Description.—Endocarp single-seeded, bilaterally symmetrical, tear-dropshaped, pointed apically, rounded basally, subtriangular in cross section, with a convex, rounded dorsal face and two more or less flat ventral faces meeting in a median longitudinal angle of 70–90°, this angle sharper above the placenta; length 4.7–8.7, avg. 6.0 mm (SD=0.97, n=42), width 2.8–5.7, avg. 4.3 mm (SD=0.82, n=42), thickness 2.2–4.9, avg. 3.7 mm (SD=0.85, n=42); transverse placental slit concave upwards, located centrally on the ventral angle of the endocarp; endocarp wall 0.3 mm thick, composed of more or less isodiametric sclereids 15–35 μm in diameter; exocarp not anatomically preserved, but showing a reticulum of coarse vascular bundles developed on dorsal and ventral surfaces; the bundles of this reticulum becoming closer together and forming a complex at the placental area. Locule casts similar in shape to the endocarps, with more pronounced ventral concavity in the position of placental slit, a sharper (less rounded) ventral angle, a more pointed apex, and a curved ridge near the base of the dorsal side corresponding to the edge of the germination valve.

Specimens.—Holotype: USNM 424885. Paratypes: HU 60010, UCMP 10655–10660, UF 6647–6648, 6657–6663, USNM 326717 (Bones, 1979, pl. 3, fig. 7, lower left), 326718 (Bones, 1979, pl. 3, fig. 7, lower right), 355491, 424877–424884, 424886–424888, 434951–434960, 434964.

Discussion.—*Bursericarpum oregonense* is represented by numerous chalcedony locule casts (Pl. 8, figs. 16, 17), occasional permineralized endocarps (Pl. 8, figs. 6–10, 12, 15), and a few complete fruit casts. The rounded angles of the endocarps suggest that they were borne freely (not fused) within the fruit. In addition, complete fruit casts with the reticulate-veined exocarp intact (Pl. 8, figs. 13, 14) show only a single endocarp per fruit. The absence of fruit casts bearing two or more endocarps suggests that fruits of this species were typically single-seeded, a feature of the tribe Bursereae.

Among extant genera, *Bursericarpum oregonense* most closely resembles *Protium*, *Tetragastris* and *Bursera*. Endocarps of *Protium* and *Tetragastris*, of the tribe Protieae, generally are larger than the fossils, and are often borne two or more per fruit. *Bursera* endocarps are borne one-per-fruit and are similar in size to the fossil. This species is particularly similar in endocarp morphology to the London Clay fossil *Bursericarpum aldwickense* Chandler (1961b). A separate species name is necessary, however, because exocarp vasculature, and the number of pyrenes per fruit, are unknown in *B. aldwickense* and because features of the seed, readily apparent in the London Clay material, are not known for the Nut Beds specimens.

Bursericarpum sp.

Plate 8, figures 18, 19

Description.—Endocarp single-seeded, bilaterally symmetrical, tear-drop-shaped, pointed apically, rounded basally, subtriangular in cross section, with a convex, rounded dorsal face and two more or less flat ventral faces meeting in a median longitudinal angle of 70–90°, length 2.0–3.2 mm, avg. 2.8 mm (SD=0.5, n=5), width 1.3–2.3 mm, avg. 1.9 mm (SD=0.4, n=5), thickness 1.0–2.0, avg. 1.6 mm (SD=0.4, n=5); placental slit transverse, located centrally on the ventral angle of the endocarp, curved apically through the endocarp.

Specimens.—UF 6654–6656, USNM 434961, 434963.

Discussion.—This species is based upon specimens that are morphologically very similar to *Bursericarpum oregonense*, but which are much smaller. Most are preserved as chalcedony casts of the endocarp; locule casts have not been observed. It is possible that these specimens may be immature or abortive endocarps of *B. oregonense*.

Family **CORNACEAE** Dumort.

The Cornaceae, or dogwood family includes six extant genera: *Cornus*, *Mastixia*, *Nyssa*, *Camptotheca*, *Davidia* and *Diplopanax* (Eyde, 1988; Eyde and Xiang, 1990). Although *Nyssa* and *Davidia* have often been segregated as Nyssaceae, Eyde (1988) reviewed the criteria used to separate Cornaceae and Nyssaceae and found them inadequate to support the continued recognition of Nyssaceae. Most species of the Cornaceae are arborescent and are distributed from temperate to tropical regions. The Nut Beds assemblage includes both extant and extinct genera of the family: *Cornus*, *Mastixia*, *Mastixioidiocarpum*, *Mastixicarpum*, *Langtonia* and *Nyssa*. Other relatives of Cornaceae present among the Nut Beds fruits include Alangiaceae (p. 34) and Hydrangeaceae (p. 50).

Genus **CORNUS** L.

Cornus clarnensis sp. nov.

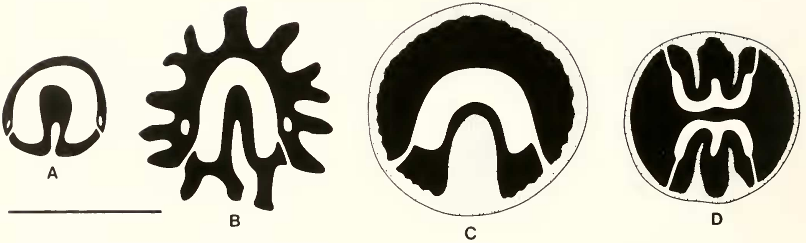
Plate 9, figures 1–15

Etymology.—The epithet is named after Clarno, Oregon, the small settlement west of the Nut Beds.

Description.—Endocarp nearly globose to ellipsoidal, bilocular (to trilocular), length 4.2, 4.4, 5.0 mm, width 3.8, 4.4, 4.3 mm; length/width ratio 1.0–1.3; base rounded, apex obtusely pointed; surface with ca. 10 fine longitudinal grooves; endocarp wall 0.5–0.6 mm thick, without lacunae, composed of more or less isodiametric polygonal sclereids, 38–70 μm in diameter, decreasing in size toward the outer surface; septum 0.2–0.25 mm thick without central vascular strand but with two peripheral vascular strands forming prominent longitudinal grooves along the endocarp surface in plane of the septum; locule lining uniseriate, composed of thin-walled cuboidal cells 45 μm in diameter along the distal surface of the locule and 25 μm on the proximal surface (nearest the septum); each locule with one seed.

Specimens.—Holotype: USNM 422378. Paratypes: UF 6310, 9763, USNM 355397, 424702.

Discussion.—*Cornus clarnensis* is represented only by five specimens: a chalcedony endocarp cast and four permineralized endocarps. Among the four specimens with internal structure preserved, three are bilocular (e.g., Pl. 9, figs. 7, 8) and the other is trilocular, but otherwise identical in anatomy (Pl. 9, fig. 12). The lack of a central vascular bundle in the septum supports placement in Cornaceae. The species corresponds to extant *Cornus* in the smooth ellipsoidal outline of the endocarp, the number of locules and the isodiametric sclereids making up the endocarp. Based upon analysis of many characters of extant species, Eyde (1988) divided *Cornus* into two groups that he named infor-



Text-figure 10.—Mastixioid fruits from the Nut Beds. **A**, *Mastixia* sp. **B**, *Mastixioidiocarpum oregonense* Scott. **C**, *Mastixicarpum occidentale* sp. nov. **D**, *Langtonia bisulcata* Reid and Chandler. Epicarp stippled where preserved. Scale bar = 1 cm.

mally according to the color of their fruits, the Blue line (ca. 50 spp.), and Red line (ca. 15 spp.). In shape and distribution of surface grooves, *C. clarnensis* resembles extant *C. florida* L., a member of the "big-bracted" subgroup of the "showy bract" group of the red line dogwoods (sensu Eyde, 1988). The fossil is distinguished from endocarps of the Cornelian cherry subgroup (or "dunstania" type) by the absence of lacunae in the endocarp wall.

A thorough review of the fossil record of *Cornus* was presented by Eyde (1988). *Cornus clarnensis* appears to be the oldest known fruit record of the big-bracted dogwoods. However, multilocular *Cornus* endocarps of the dunstania type occur in the late Paleocene of North Dakota (Crane et al., 1990) and in the early Eocene London Clay flora (Eyde, 1988). Although Reid and Chandler (1933) attributed the London Clay species to an extinct genus, *Dunstania*, Eyde (1988) argued that the "dunstanias" belong within *Cornus* and, because of lacunae in the endocarp wall, correspond to the Cornelian cherry subgroup.

Genus **MASTIXIA** Blume

Mastixia is an extant tropical genus of 13 species distributed in Indomalesia. Several fossil species of *Mastixia* (reviewed by Kirchheimer, 1957; Mai, 1970) and closely related extinct genera (Kirchheimer, 1936, 1957) are common in the middle to late Tertiary of central Europe, prompting application of the term "Mastixoid flora" to these warm-climate fossil assemblages (Kirchheimer, 1940). Knobloch and Mai (1986) reported several species of this complex from the Late Cretaceous (Maastrichtian) of Germany and presented a key distinguishing the European fossil mastixioid genera. The mastixioid group is represented in the Nut Beds flora by *Mastixia*, *Mastixioidiocarpum*, *Mastixicarpum*, and *Langtonia*.

Mastixia sp.

Plate 10, figures 1–3; Text-figure 10A

Description.—Endocarp ovoid, unilocular, single-seeded, surface smooth; length 8.0–11.5 mm (estimated from incomplete specimens), width 5.7–7.0, avg. 6.3 mm (SD=5.7, n=5), dorsiventral thickness 6.0–6.7, avg. 6.4 mm (SD=0.33, n=4); dorsal surface with a sulcus formed by a deep longitudinal infold of the endocarp wall extending about 2.8 mm into the locule; infold thick (1.8–2.4 mm); locule U-shaped in cross section; endocarp wall 0.6–0.8 mm thick, composed of two layers: the inner layer 0.3–0.4 mm thick with fibers 14–20 μm in diameter and more than 400 μm long, mostly oriented transversely; outer layer approximately the same thickness, 0.3–0.4 mm, composed of more or less isodiametric to elongate sclereids, 20–35 μm wide and up to 200 μm long; germination valve elongate; dehiscence plane running nearly the full length of the endocarp, extending from the dorsal limbs of the locule through the thickness of the endocarp wall; two longitudinal lacunar tubes up to 0.5 mm in diameter situated parallel and adjacent to the dehiscence plane, one on each side of the locule; epicarp not preserved. Locule cast ellipsoidal, concave dorsally, trough-shaped, base rounded, apex pointed; length 7.3 mm, width 4.8 mm, thickness 4.1 mm.

Specimens.—UF 6303, 6502, 9369, 9470, permineralized endocarps; USNM 354035, locule cast.

Discussion.—This species, represented by a few permineralized endocarps and a locule cast, conforms to extant *Mastixia* on the basis of its relatively smooth endocarp surface, the dorsal infold and germination valve and the anatomical structure of the endocarp consisting of an inner layer of transversely aligned fibers surrounded by an outer layer of sclereids (Pl. 10, fig. 3). Kirchheimer (1936, pl. 5, fig. 10) and Eyde

(1963) illustrated endocarps of comparable living species including *M. trichotoma* Blume. Eyde (1963) observed that: "the endocarp splits exactly where two ovular traces pass through the endocarp from base to placenta. These vascular strands form hollow space where the ovular trace deteriorates". The same structures are observed in the fossil (Pl. 10, fig. 2; Text-fig. 10A) and are described above as lacunar tubes. The dorsal infold is much thicker in this fossil than in most extant species. However, the two species of subgenus *Manglesia* (*M. euonymoides* Prain and *M. octandra* Matthew), which I have not seen, are described as having thick infolds ("septum swollen to one third the diameter of the fruit", Matthew, 1976).

This species differs from the other Clarno mastixioid species by its smaller size, thinner endocarp wall and smooth surface. The lack of preserved epicarp (mesocarp and exocarp) may indicate that the outer layers were fleshy and hence lost prior to fossilization. The smooth surface of the endocarp and small size differentiates this species from the nodular surfaced endocarp of *Mastixia cantiensis* and from the gently ribbed *M. parva* from the London Clay flora (Reid and Chandler, 1933).

Genus **MASTIXIOIDIOCARPUM** Scott

Mastixioidiocarpum oregonense Scott

Plate 10, figures 4–11, Text-figure 10B

Mastixioidiocarpum oregonense Scott 1954, p. 84, pl. 16, figs. 16–18.

Emended Description.—Fruit ovoid, rounded apically and basally, unilocular, single-seeded, length 13–23.8, avg. 20.2 mm (SD=3.91, n=6), width 9.2–15, avg. 11.7 mm (SD=2.01, n=8), dorsiventral thickness 8.2–15.0, avg. 11.6 mm (SD=2.45, n=7); endocarp longitudinally ribbed with nine to 14 prominent irregular sharp ridges up to 1.5 mm in relief that are irregularly divided into excrescences or protuberances; endocarp surface with a dorsal sulcus (longitudinal infold) extending 3.8–5.8 mm into the locule (hence, locule U-shaped in cross section); endocarp wall 2.5–4 mm thick measured to the crest of the highest ribs; germination valve elongate; dehiscence plane running nearly the full length of the endocarp, extending from the dorsal limbs of the locule through the thickness of the endocarp wall; two longitudinal lacunar tubes up to 0.5 mm in diameter running through the endocarp adjacent to the dehiscence plane, one on each side of the locule; endocarp consisting of an inner layer 0.3 to 0.4 mm thick made up of horizontal, periclinally oriented fibers, 17–23 μm in diameter, grading into the outer layer 2.2–3.7 mm thick composed of fibers, 28–60 μm in diameter, arranged in tracts of varying orientation; locule lining formed by transversely aligned cells; epicarp not preserved. Locule cast narrowly saddle shaped, the ventral face convex, the dorsal face concave, U-shaped in transverse section, the arms proximate, lateral margins rounded, but thinning toward the ends and acute at base and apex, traces of a median raphe strand visible on the ventral surface.

Specimens.—Holotype: UM 29938. Hypotypes: HU 60013, OMSI Pb196, UF 9206–9208, 9210, 9269, USNM 354022–354028 (these specimens together in the same piece of matrix), 354029, 354031, 354033, 354034, 354036, 354037, 354598, endocarps; UCMP 10661, 10662, USNM 354036, 354038, 354039 (3 specimens), 354041 (3 specimens) 354042, 354049, locule casts.

Discussion.—*Mastixioidiocarpum oregonense* is distinguished from the other mastixioids of the Nut Beds by its prominently sculptured endocarp surface (Pl. 10, figs. 4, 8; Text-fig. 10B). It is preserved as permineralized endocarps, locule casts and endocarp molds. Commonly, the endocarp itself has disintegrated, leaving behind its mold in the matrix, with a chalcedony locule cast inside. In one such example, the locule cast was removed (Pl. 10, figs. 9–11) and a replica of the original endocarp, complete with the irregular surface ribs, was prepared by making a latex cast of the surrounding sedimentary mold (Pl. 10, fig. 8). Molds with the same distinctive type of sculpture are known from other localities of the Clarno Formation, including West Branch Creek, Gosner Road, and from the Eocene Sepulcher Formation of Yellowstone National Park (Princeton 22488, specimen at USNM).

These endocarps are morphologically similar to those of extant *Mastixia*, but differ by the prominent, coarse sculpture and thick fruit wall. Scott (1954) established the genus *Mastixioidiocarpum* for this Nut Beds species, because not enough details were preserved to enable a secure assignment to any of the extinct genera known from the European Tertiary (Kirchheimer, 1936; Reid and Chandler, 1933). Since Scott's work was published, however, many additional specimens have been recovered, some with excellent anatomical detail, enabling a more informed comparison with other fossil and modern material. The resulting new information, included in the above description, supports retention of the generic name *Mastixioidiocarpum*, because the Clarno fossil is readily distinguished in its morphology from the European fossil mastixioid genera reviewed by Holý (1975) and Knobloch and Mai (1986). In sculpture and thickness of the endocarp, *Mastixioidiocarpum* resembles *Eomastixia* Chandler (= *Ganitrocera* Kirchheimer) as emended by Holý (1975). However, *Eomastixia* generally is two-loculed (up to four-loculed) and, when unilocular, there is usually evidence of an abortive ovule (Holý, 1975). *Mastixioidiocarpum* specimens are exclusively unilocular, without any indication of an abortive ovule.

Genus MASTIXICARPUM Chandler

Mastixicarpum occidentale sp. nov.
Plate 10, figures 12–15; Text-figure 10C

Etymology.—*Occidens* (L = of the west), referring to the western occurrence of this species.

Description.—Fruit ovoid, unilocular, length 21.0–22.0 mm, width 14.5–16.0 mm, dorsiventral thickness 11.8–15.5 mm; endocarp with faint longitudinal ridges; dorsal infold present but not well exposed surficially; infold extending 6 mm into the locule; endocarp wall 3.6–4.0 mm thick, composed of interwoven tracts of fibers, the fibers 38–80 μm in diameter; vascular bundles located in a narrow zone transitional between endocarp and epicarp; epicarp surface smooth, exocarp 0.8–1.0 mm thick, composed of anticlinally elongate sclereids, 28–55 μm in diameter, 80–300 μm long. Locule boat-shaped, the dorsal face concave, and the ventral convex, c-shaped in cross section; dehiscence plane running nearly the full length of the endocarp, extending from the dorsal limbs of the locule through the thickness of the endocarp wall.

Specimens.—Holotype: UF 8740. Paratype: UCMP 10705.

Discussion.—This species is known from two fragmentary but well preserved permineralized specimens from the Nut Beds, and by a well preserved specimen from the Brummers's Spring Clarno locality (UF 9886; loc. 254). *Mastixicarpum occidentale* differs from the other Clarno mastixoids by the presence of a resistent epicarp (Pl. 10, figs. 13–15, Text-fig. 10C). The epicarp in the other species was probably fleshy and easily degraded as in extant *Mastixia*. The endocarp of this species is smooth in comparison to the strongly ribbed endocarps of *Mastixioidiocarpum* discussed above.

Among fossil mastixioids recognized in the Tertiary of Europe, four genera have persistent epicarps (Knobloch and Mai, 1986): *Mastixicarpum* Chandler, *Mastixiopsis* Kirchheimer, *Retinomastixia* Kirchheimer, and *Tectocarya* Kirchheimer. Of these, the Nut Beds species most closely resembles *Mastixicarpum* and *Tectocarya*. *Tectocarya* has a pair of lacunae separated by a median septum in the upper ⅔ of the dorsal infold, and has a thin epicarp that may become free from the endocarp, whereas *Mastixicarpum* lacks the longitudinal septum in the infold and has a thick epicarp that is tightly attached to the endocarp. Based upon sections of *Tectocarya rhenana* Kirchheimer that I have examined from Düren, Germany, there are no prominent secretory ducts, and the epicarp is composed of very small isodiametric cells. The Clarno species corresponds most closely in morphology and anatomy to *Mastixicarpum*, based upon sections of *M. limnophilum* that I have examined from the Miocene of Wiesa, Germany. The two species correspond in thickness of the epicarp, size and orientation of epicarp cells, and in the presence of secretory canals at the junction of the endocarp and epicarp.

Recent recognition of the extant Chinese genus *Diplopanax* as a living mastixioid (Eyde and Xiang, 1990) is of considerable interest in interpreting paleobotanical remains. *Diplopanax*, like *Mastixia*, has an ovoid unilocular fibrous endocarp with an elongate dorsal germination valve. Although there is a dorsal infold resulting in a locule that is u-shaped in cross section, the infold is not apparent at the surface of the endocarp, which has a circular cross section. *Mastixia* fruits have a soft epicarp, whereas that of *Diplopanax* is woody or leathery. Also, the endocarp of *Diplopanax* is riddled with longitudinal secretory canals that are not observed in the endocarp of *Mastixia*. Eyde and Xiang (1990) suggested that *Mastixicarpum* and *Diplopanax* are equivalent. However, in both *Mastixicarpum limnophilum* and *M. occidentalis* the secretory canals are mostly peripheral to the endocarp (e.g., Pl. 10, fig. 15), largely confined to the epicarp, whereas in *Diplopanax stachyanthus* Hand.-Mazz. the secretory canals are uniformly distributed, giving a speckled appearance to the endocarp in cross section.

Genus LANGTONIA Reid et Chandler

Langtonia bisulcata Reid et Chandler
Plate 11, figures 1–10; Text-figure 10D

Langtonia bisulcata Reid et Chandler 1933, p. 453, pl. 25, fig. 18–27.

Description.—Fruit oblong, more or less circular in cross section, rounded basally and apically, length 16.0–35.0, avg. 24.9 mm (SD=5.27, n=7), width 10.0–26.5, avg. 14.8 mm (SD=4.56, n=7), dorsiventral thickness 9.9–22.0, avg. 14.1, mm (SD=4.12, n=7); bicarpellate, with two single-seeded elongate locules, sometimes with one of the locules poorly formed, abortive; locules w-shaped in cross section, due to a pair of longitudinal infolds of the endocarp wall; longitudinal planes of dehiscence in the endocarp wall defining a pair of germination valves, one corresponding to each locule; each germination valve extending the full length of the locule, similar in width to the locule that it serves; septum without a central vascular column; endocarp made up of tracts of fibers oriented in various directions; epicarp about 1 mm thick, composed of thin-walled, periclinally elongate cells 20–30 μm high and 40–120 μm wide;

secretory ducts present both in endocarp and epicarp; seeds conforming in shape to the locule. Locule casts elongate, dorsiventrally flattened 12.5–20.6 mm long, 5.5–12.7 mm wide, 2.2–6.0 mm thick, pointed apically and basally, sometimes with fine transverse striations; dorsal side with a median longitudinal ridge flanked on either side by a prominent groove, ventral side convex-rounded with a thread-like median longitudinal raphe groove or ridge.

Specimens.—HU 60016, UF 8729–8735, 8740, 8742, USNM 312746 (Bones 1979, pl. 4, fig. 5 top), 354032, 354046, 354052, 354053, 354351, 354423, 354937, 354941, 422524, 424810, 424875, endocarps; UF 8736–8739, USNM 312747 (Bones 1979, pl. 4, fig. 5, left), 354043, 354047, 354050, locule casts. Holotype: BM v22984 from the London Clay.

Discussion.—*Langtonia* is represented in the Nut Beds by permineralized endocarps (Pl. 11, figs. 1–3) and occasional isolated locule casts (Pl. 11, figs. 5, 6). Fruits have been recovered from the basal leaf layer of Face 3, as well as higher in the Nut Beds section. The preservation of fruit morphology and anatomy is excellent as seen in transverse sections (Pl. 11, figs. 4, 7–10).

This species was first described and recognized as an extinct genus from the London Clay flora by Reid and Chandler (1933). They attributed *Langtonia* to the Cornaceae and placed it near *Mastixia* because of its long, infolded germination valves. It differs from *Mastixia* in having two infolds of the locule, rather than one, resulting in a w-shaped, rather than u-shaped, cross section. Kirchheimer (1936) expressed doubt as to the mastixioid affinities of this genus. Anatomy revealed in peels of the well preserved Clarno material (Pl. 11, figs. 9, 10), however, shows variously oriented tracts of fibers forming the endocarp in conformity with the anatomy of *Mastixia*, *Diplopanax* and *Nyssa*. In addition, the presence of secretory canals in the endocarp and epicarp is a feature shared with *Diplopanax* and *Mastixicarpum*. Therefore, *Langtonia* should be reinstated as a member of the Cornaceae.

Most of the Nut Beds endocarps are larger than those described by Reid and Chandler (1933) from the London Clay (length 9–20, avg. 15.5 mm; width 4.5–12, avg. 9.6 mm). The size ranges overlap, however, and the specimens are morphologically indistinguishable, and I have therefore placed the Nut Beds specimens in the same species.

Genus NYSSA L.

Nyssa spatulata (Scott) comb. nov.
Plate 11, figures 11–19

Palaeonyssa spatulata Scott 1954, p. 83, pl. 16, fig. 8–12.

Description.—Endocarp oblong, ovoid or ellipsoidal, trilocular, roughly circular to rounded-triangular in cross section, base and apex rounded, with nine rounded longitudinal ridges extending from base to apex, length 20.1–30.0, avg. 24.0 mm (SD=3.8; n=15), width 12.0–21.5, avg. 14.6 mm (SD=2.8, n=16), endocarps trilocular, with large, rounded germination valves visible as slits in the apical half of the endocarp; wall and septa composed of swirling tracts of fibers, the fibers 15–30 μm in diameter; central axis not vascularized, epicarp not preserved. Locules single-seeded, elongate, spatulate, c-shaped in cross section, concave outward, broadening and rounded apically, narrowed and pointed basally.

Specimens.—Holotype: UM 29936 (Scott, 1954, pl. 16, fig. 8, 9). Paratype: USNM 40543 (Scott, 1954, pl. 16, fig. 10–12). Hypotypes: OMSI Pb197A, Pb914, UF 6834–6842, USNM 354541, 354582–354584, 354586, 354591, 354594, 354595, 354604, 424874.

Discussion.—This species was described by Scott (1954) on the basis of four specimens. Although it is not abundant in the assemblage, it is now known from approximately 25 specimens, resulting in the broader range of dimensions indicated in the above description. All of the specimens show three locules (rather than three to four as in the London Clay species).

Reid and Chandler (1933) correctly deduced the close affinity of this taxon to extant *Nyssa*, but because of some apparent differences, particularly the presence of three to four locules, placed the London Clay fossils in a new genus, *Palaeonyssa*. Scott (1954) recognized close similarity between the Clarno and London Clay fruits, and placed the Nut Beds specimens in a new species of *Palaeonyssa*. These fossils differ from most modern species of *Nyssa* in being consistently trilocular (Pl. 11, figs. 16–18), rather than unilocular, and by their larger size. Thin sections reveal that the endocarp is made up of swirling fibers (Pl. 11, fig. 19), as is also true of extant species of *Nyssa*.

Nyssa has about six extant species (three in North America, one in China, one in Indomalesia and one in southern Central America) that are readily distinguished from one another on the basis of fruit morphology (Eyde, 1963). The new discovery of an extant species of *Nyssa* from Costa Rica and Panama, *N. talamancana* Hammel and Zamora (1990), is helpful in the interpretation of fossil remains. Fruits of *N. talamancana* measure 4–5 cm in length and 2–2.5 cm in diameter, and are larger than those of any other living or fossil species of the genus. In contrast to the other extant species of *Nyssa*, which typically have only one locule, and in rare instances two locules (Eyde, 1963), stones of *N. talamancana* are bilocular to trilocular (Hammel and Zamora, 1990). Taking into consideration the wider range of endocarp morphology imparted to *Nyssa* by the tropical American species, the taxon *Palaeonyssa* now appears to fall neatly within the extant genus.

Nyssa scottii sp. nov.
Plate 12, figures 1–2

Etymology.—This species is named for Richard A. Scott in recognition of his careful work on the Clarno fruit and seed flora.

Description.—Endocarp spindle shaped, fusiform in lateral view, roughly circular in cross section, trilocular, base and apex bluntly pointed, surface with coarse meridional ribs; length 12.6–16.5, avg. 13.8 mm (SD=2.3, n=6), width 6.1–9.5, avg. 7.5 mm (SD=1.18, n=6), endocarp with three inverted u-shaped germination valves over the apical ⅓ of the endocarp; endocarp wall 1.2 mm thick composed of fibers 12–30 μm in diameter, arranged in swirling groups, central axis not vascularized.

Specimens.—Holotype: USNM 354588. Paratypes: OMSI Pb207, UF 6843, USNM 354582, 354600, 435150.

Discussion.—*Nyssa scottii* is represented by several translucent silica casts and one permineralized specimen (UF 6843). The shape, size, surface sculpture and type of germination valve are diagnostic of *Nyssa*. The specimens are tricarpellate as in *N. spatulata*, rather than unicarpellate as is the usual condition in extant species. One of the specimens (Pl. 12, figs. 1, 2) has one of the germination valves broken away, showing a locule that is D-shaped in cross section with the convex surface inward. The short length of the germination valves is a character that distinguishes *Nyssa* from the mastixioid genera (Chandler, 1926, pp. 36–37). This species is readily distinguished from *N. spatulata* by its smaller size range (length 12–17, vs. 20–30 mm).

Nyssa sp.
Plate 12, figures 3–5

Description.—Fruit unilocular, endocarp more or less elliptical in face view, dorsiventrally compressed, rounded basally, dorsal side convex, ventral side concave; length 24.6, 30.0, 48.0 mm (est. from incomplete specimen), width 12.9, 23.5, 25.0 mm, dorsiventral thickness 5.1, 12.6, 10 mm, surface relatively smooth, with thin, shallow longitudinal grooves; endocarp wall 3.2 mm thick, composed of tracts of swirling fibers, the fibers 15–30 μm in diameter. Locule cast dorsiventrally compressed.

Specimens.—UF 9757, UM 66135, USNM 446088.

Discussion.—Three unilocular specimens of *Nyssa* have been recovered from the Nut Beds. The longitudinal grooves on the endocarp (Pl. 12, fig. 3) and thick wall composed of swirling tracts of fibers (Pl. 12, fig. 5), are consistent with assignment to *Nyssa*. There is no indication of abortive locules and, in the absence of any bilocular specimens in the Nut Beds collections, it seems likely that this represents a species distinct from the trilocular species, *N. spatulata* and *N. scottii*. Although it is incomplete, the larger of the specimens (Pl. 12, fig. 3) appears to have been longer than any of the trilocular specimens.

The relatively smooth surface, size, and marked dorsiventral compression of these endocarps suggests affinities with *N. brandoniana* (Lesquereux) Eyde and Barghoorn, from the Brandon lignite of Vermont (Eyde and Barghoorn, 1963) and extant *N. javanica* (Bl.) Wangerin of southeast Asia and Malesia (Eyde, 1963).

Family **FAGACEAE** Dum.

The Fagaceae (oak family) are represented in the Nut Beds by at least two genera of fruits: *Quercus*, and *Castanopsis*. Two kinds of fagaceous foliage have been recovered from the Nut Beds (Manchester, 1981). In addition, two species of fagaceous wood have been recognized (Scott and Wheeler, 1992): *Quercinium crystallifera*, with anatomy corresponding both to extant *Lithocarpus* and to evergreen species of *Quercus*, and *Fagaceoxylon ostryopsoides*. *Fagaceoxylon* Scott et Wheeler is an extinct genus with characters diagnostic of fagaceous wood including aggregate rays, opposite to alternate intervascular pitting, mostly simple perforation plates, vasicentric tracheids and variable ray-vessel parenchyma pits. As noted by Scott and Wheeler (1982), however, the pore arrangement of *Fagaceoxylon*, i.e., diffuse porous with radial multiples and clusters arranged in "flame-like" tracts, is unknown in any living genus.

The Fagaceae have an excellent fossil record in the Tertiary of the northern hemisphere (Daghlian and Crepet, 1983; Crepet and Nixon, 1989 a, b; Kvacek and Walther, 1989). The Nut Beds flora provides the oldest known fruit records of *Quercus* and *Castanopsis*.

Genus **CASTANOPSIS** (D. Don) Spach.

Castanopsis crepetii sp. nov.
Plate 12, figures 6–11

Etymology.—This species is named after William Crepet, recognizing his contributions to the North American fossil record of Fagaceae.

Description.—Fruit a globose nut completely enveloped by cupule, length (15)–39 mm, equatorial diameter (15)–36 mm; base and apex rounded, surface coarse; nutshell 1.8–2.0 mm thick, composed of isodiametric angular sclereids 12–50 μm in diameter organized concentrically into islands of densely packed cells among smaller cells, with occasional vascular bundles passing through the nutshell; cupule adnate to the nut, 1.8–2.0 mm thick, composed of similar, less densely packed cells. Locule cast rounded-conical, truncate basally, pointed apically, with meridional grooves defining broad-rounded ridges.

Specimens.—Holotype: UF 9267, large permineralized fruit. Paratypes: UF 9268, USNM 354811, 446079, fruits; UF 9597, 9598, locule casts.

Discussion.—This species is represented by permineralized fruits and occasional locule casts. The holotype is a large, fragmentary permineralized specimen showing the globose outer surface of the cupule (Pl. 12, fig. 6), with portions of the cupule and nutshell removable to show the apically tapered, basally truncate, locule cast with longitudinal grooves (Pl. 12, figs. 7, 8). Thin sections of the wall clearly show the junction of cupule with the nut (Pl. 12, figs. 9, 10).

In the Fagaceae, some species of both *Castanopsis* and *Lithocarpus* have globose nuts with complete cupular coverage and adnation between the nut and cupule (Camus, 1952–54; Kaul, 1988, 1989). These genera apparently overlap with one another, as summarized by Kaul (1989, p. 68): "Generic and infrageneric taxonomy in the *Lithocarpus–Castanopsis* complex has a long history of instability (Forman, 1966). Some recent authors have accepted the two genera in their broad senses, acknowledging some species with intermediate character states."

Castanopsis piriformis Hick. et A. Camus from Annam, southern Vietnam (Pl. 12, figs. 12–15) is an extant species that resembles *C. crepetii* in size, globose shape of the fruit, wall structure and locule morphology. Transverse sections of the endocarps of these two species reveal remarkable similarity, both at the macroscopic and microscopic levels. In both the fossil and the modern species, adnation of cupule and nut is clearly evident (Pl. 12, figs. 9, 14) and the nutshell wall is made up of more-or-less angular sclereids that are grouped concentrically to form conspicuous "islands" as viewed in transverse section (Pl. 12, figs. 11, 15). The anatomical correspondence confirms the identity of this fossil to the Fagaceae, and supports placement within *Castanopsis* (providing that the generic assignment of *C. piriformis* is correct). *Castanopsis* also has a good fossil fruit record in Europe based upon species with small, angular nuts (Mai, 1989).

Genus **QUERCUS** L.

Quercus paleocarpa Manchester
Plate 12, figures 16–18

Quercus paleocarpa Manchester, 1976, p. 82, pl. 5, fig. 29.

Description.—Acorn with prolate to ovate nut covered ⅓ to ½ from base to apex by a thick woody cupule; complete fruit length (nut with cupule) 22 mm, width 15.5–21.8 mm; nut length (without cupule) 14.0–18.0, width 11.4–15.6 mm; nut base rounded, apex obtuse; relatively smooth, finely longitudinally striate; cupule bowl-shaped, height 9.0–10.4 mm, width 18–21 mm, with seven concentric exterior transverse ribs; the ribs decreasing in thickness from the base to the apical rim.

Specimens.—Holotype: OMSI Pb176, nut with abraded cupule. Hypotypes: USNM 414508, isolated cupule; USNM 312758 (Bones, 1979, pl. 6, fig. 9), complete, abraded nut.

Discussion.—This species, representing the oldest known acorn, is represented only by a few specimens. The most complete specimen, with both the nut and cupule intact (Pl. 12, figs. 16, 17) was abraded prior to deposition, so that the arrangement of involucral scales on the outer surface of the cupule cannot be determined. A well-preserved detached cupule (Pl. 12, fig. 18) shows the outer surface in an unworn condition, revealing involucral scales arranged in concentric rings. I assume that each of these specimens represents the same species, although a larger population would be desirable to rule out the possibility that two different taxa are present.

Although the cupules of extant species of *Lithocarpus* and *Quercus* are often indistinguishable (Kaul, 1988), the coarse, rather than papery, lamellae of the cupule and the limited extent to which the cupule covers the nut suggest that the species belongs to *Quercus* rather than *Lithocarpus*. Cupules with the involucre arranged in concentric rings as in this fossil occur in the strictly Asian subgenus *Cyclobalanopsis* of *Quercus*, as well as in *Lithocarpus*.

Nixon (1989) noted that the cyclic arrangement of cupule scales/spines, which also occurs in *Chrysolepis*, *Castanopsis*, *Castanea* and *Trigonobalanus*, is apparently pleisiomorphic within the Fagaceae, with the imbricate-spiral arrangement found in the derived forms of *Quercus*. If this interpretation is correct, then it is not surprising that *Quercus paleocarpa*, the oldest known *Quercus* fruit, should possess a cupule with cyclically arranged scales.

Family **FLACOURTIACEAE** DC.

The Flacourtiaceae are a family of about 90 genera and about 875 species of shrubs, less often trees, that are chiefly tropical in distribution, but with a few that are temperate. The species described below, belonging to an extinct genus, is the only member of this family recognized from the Nut Beds. The extant genus *Oncoba*, recognized in the London Clay flora (Reid and

Text-figure 11.—*Saxifragispermum tetragonalis* sp. nov., transverse section showing four-valved capsule with parietally attached seeds.

Chandler, 1933) does not appear to be present in the Nut Beds collections.

Genus **SAXIFRAGISPERMUM** Reid et Chandler

Saxifragispermum tetragonalis sp. nov.

Plate 13, figures 1–16; Text-figure 11

Etymology.—*Tetra* (Gr = four) + *gonia* (Gr = angle, corner), referring to the four-angled shape of the fruit.

Description.—Fruit an elongate-obovoid, tetracarpellate, tetravalved loculicidal capsule, nearly circular to rounded-quadrangular in cross section; length 6.4–11.8, avg. 9.2 mm (SD=1.42, n=20), width 3.0–5.6, avg. 4.2 mm (SD=0.63 n=19); base more or less rounded, sometimes with a small projection at the pedicel scar, apex pointed; placentation parietal, with four elongate placental ribs, one positioned medially on each of the four valves of the fruit and extending the full length of fruit; seeds numerous, six to eight radiating from any given level on the placenta, arranged vertically in rows about 12 high; interior of fruit solid with sinuously arranged fibers 5–18 μm in diameter having a general longitudinal orientation, among which the seeds are embedded; fruit wall comprised of two layers: inner layer forming a thin lining (80–120 μm thick) of longitudinally oriented fibers 12–30 μm in diameter (this is the layer that forms the placental ribs), outer layer (150–200 μm thick) formed of similar fibers oriented horizontally and periclinally; this outer layer showing lines of loculicidal dehiscence; pedicel scar with five apertures, one central, and four lateral, representing extensions of the placentae. Seeds ovoid, ascending, rounded basally, tapered apically, 0.5–0.7 mm long, 0.35–0.45 mm wide; seed coat composed of an outer layer of mostly quadrangular cells about 15–20 μm wide producing small spine-like simple hairs 18–25 μm long and an inner layer of transversely elongate hexagonal cells about 35–40 μm wide and 12–14 μm high.

Specimens.—Holotype: UF 5236 (Bones, 1979, pl. 4, fig. 4). Paratypes: UCMP 10614–10617, UF 6312, 6471, 6473–6478, 6575, 6649–6653, 6972, 9897, USNM 353999, 354000 (21 specimens), 354001 (7 specimens), 354002 (2 specimens), 354006–354008, 354009 (7 specimens), 354010 (2 specimens), 354011, 355469.

Discussion.—This species is represented by numerous permineralized specimens and occasional casts. Part of the outer wall is often stripped away when the specimens are removed from the matrix, sometimes showing the rows of seeds (Pl. 13, figs. 3–5). Serial transverse sections reveal as many as eight seeds surrounding each placenta in a single slice (Pl. 13, figs. 7–9). The placentae are preserved in white silica and appear to have been hollow or parenchymatous (Pl. 13, fig. 9). Scanning electron microscopy of fractured specimens illustrates details of the seeds and surrounding fibers (Pl. 13, figs. 11–14).

These valvate capsules resemble the fruits that Reid and Chandler (1933) named *Saxifragispermum spinosissimum* (emended diagnosis Chandler, 1961b) from the London Clay. Both have median longitudinal parietal placentae with about a dozen rows of seeds on each placenta; in both taxa the entire cavity of the locule is virtually filled with fibers (Pl. 13, figs. 9, 11–13). Seeds of the London Clay fossil were originally described as spinose and small projections from the seed coat were figured by Reid and Chandler (1933, pl. 8, fig. 35). However, Chandler (1961b) redescribed the seeds more cautiously: "Testa apparently spinescent (unless this is an effect of decay)". Thin sections of the Nut beds specimens confirm the presence of small spines or spine-like trichomes on the seed coat (Pl. 13, figs. 15, 16).

Placentation and seed morphology indicate that *Saxifragispermum* is related to the Flacourtiaceae. Although the generic name suggest affinities to Saxifragaceae (Reid and Chandler, 1933), Chandler (1961a) reported that "Examination of more material and reconsideration of the whole evidence necessitates a correction of the supposed relationship to Saxifragaceae. The single locule with its broad parietal placentae bearing several rows of seeds is unlike any known Saxifragaceae, a family which normally shows two or more locules. It is highly suggestive of Flacourtiaceae. Moreover the succession of coats in the seed and the character of the chalaza are so closely comparable with the same features in *Oncoba* that the probability of relationship with Flacourtiaceae is confirmed."

Although clearly congeneric with the London Clay fruits, the Nut Beds material can confidently be regarded as a distinct species. The London Clay fruits are much wider in diameter, and have larger seeds. *S.*

spinosissimum fruits range from 11.5 to 15.75 mm, whereas those of *S. tetragonalis* range only from 6.4–11.8 mm. The London Clay fossils range from four to five carpels, whereas the many Nut Beds specimens are all tetracarpellate. *Carpolithus subfusiformis* (Bowerbank) Reid et Chandler (1933), which is known from tri- and tetracarpellate fruits, also shows similarity to and may, in fact, be conspecific with *S. spinosissimum*.

Family **HAMAMELIDACEAE** R. Br.

The Hamamelidaceae (witch hazel family), with 29 extant genera and about 90 species, is divided into four subfamilies: the Hamamelidoideae, Rhodoleioideae, Exbucklandioideae, and Liquidambaroideae (Endress, 1989a). The Liquidambaroideae are known to have been present in the Eocene based upon *Liquidambar* leaves in the Green River Formation, Utah (MacGinitie, 1969), and fruits identified as *Steinhauera* Presl from the Geiseltal of Germany (Mai, 1976), but have not been identified from the Clarno Formation. Infructescences from the Clarno Nut Beds formerly identified as *Altingia* (Scott in Chandler, 1961a; Bones, 1979) have been shown to represent *Macginitiea* (Platanaceae; Manchester, 1986). The Hamamelidoideae are represented in the Nut Beds flora by the single fruit and seed species described below, and by inflorescences that may or may not represent the same taxon (Pl. 14, figs. 14–16). The oldest fossils with close affinities to the Hamamelidaceae are flowers with intact stamens and pollen from the Late Santonian or Early Campanian of Scania, Sweden (Endress and Friis, 1990).

Genus **FORTUNEARITES** gen. nov.

Etymology.—*Fortunearites* is named for its similarity to extant *Fortunearia*.

Type species.—*Fortunearites endressii* sp. nov.

Fortunearites endressii sp. nov.
Plate 14, figures 1–13

Etymology.—The species is named for Peter R. Endress, recognizing his important contributions in understanding the systematics and phylogeny of Hamamelidaceae.

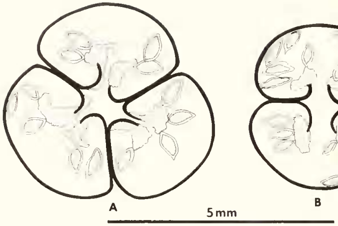
Description—Infructescence a spike, with a stout axis up to 53 mm long, 2.4 mm in diameter, bearing numerous closely packed sessile fruits; infructescence about 15 fruits in length with up to eight fruits encountered at a given level in transverse section of the axis; fruit a bicarpellate, bilocular woody capsule, quadrilaterally symmetrical, squarish in longitudinal view, elliptical in transverse section, with the long axis of ellipse parallel to the infructescence axis; capsule 5–7 mm long, 6.8–7.5 wide, 5.0–5.2 mm thick, fruit wall 0.8–1.0 mm thick; locules more-or-less pyriform, flattened ventrally where they contact the septum, single-seeded; dehiscence of capsules apical by a split bisecting each of the locules through the major plane of symmetry.

Internal molds of the seed coat obliquely ellipsoidal, asymmetrical, pointed apically, rounded basally, 5.8–6.2 mm long, 3.3–3.4 mm wide, 2.4–2.8 mm thick, length/width ratio 1.7–1.8; hilar scar not evident in these molds; surface of mold smooth except for a raised ribbon-like raphe band, 0.4–0.5 mm wide extending from the front to the back of the seed passing obliquely over the base in a u-shaped course with each limb extending ½ to ⅔ of the distance toward the seed apex.

Specimens.—Holotype: OMSI Pb156 (and counterpart, USNM 354581), permineralized infructescence. Paratypes: UF 8741, permineralized infructescence; UF 9258, 9259, locule casts; UF 6530 9330, USNM 424632, 424651, internal molds of seed coat.

Discussion.—This species is represented by two permineralized infructescences (e.g., Pl. 14, figs. 1, 2), a few locule casts (e.g., Pl. 14, figs. 6–9), and several endosperm casts (e.g., Pl. 14, figs. 10–13) from the Nut beds. Tangential sections of the infructescence intercept individual fruits transversely (Pl. 14, figs. 3, 4) showing the thick walls and bilocular construction of the capsules. Seeds are not preserved within the infructescences and it is likely that they had dispersed prior to deposition. Isolated seeds (actually internal molds of the seed coat, Pl. 14, figs. 10–13) correspond in shape and size to the locules of the infructescences. The capsule morphology matches that of extant genera in the subfamily Hamamelidoideae. Genera of this subfamily have one seed per carpel, which is ejected explosively at maturity. The large number of fruits on the axis, and seed characters discussed below, suggest affinity with extant *Sinowilsonia* and *Fortunearia*.

Endress (1989b) indicated that seeds of extant Hamamelidoideae are structurally constrained by the explosive dehiscence mechanism so that fruit and seed structure is extremely uniform throughout the subfamily, making it difficult to determine the affinities of fossil seeds down to the generic level. Subsequently, Grote (1989) found differences in hilar scar morphology among some of the extant genera that enabled recognition of *Corylopsis* seeds in the Eocene of Tennessee. In addition, I have observed differences in the course of the raphe that set *Sinowilsonia* and *Fortunearia* apart from other genera of the subfamily. In reviewing the seed anatomy of selected extant genera of Hamamelidaceae, Mohana Rao (1974) indicated that seeds of *Hamamelis, Parrotia* and *Sinowilsonia* have a raphe with vascular bundles running along one side



Text-figure 12.—Transverse sections of *Hydrangea knowltonii* sp. nov., showing deeply intruded parietal placentae and numerous seeds. **A**, Tricarpellate capsule. **B**, Bicarpellate capsule.

of the seed ending at the chalaza. In dissections of modern seeds I found that the raphe bundles indeed run their course on only one side of the seed and terminate basally in *Eustigma*, *Loropetalum*, *Matudaea*, *Parrotia*, and *Hamamelis*. However, in *Fortunearia sinensis* Rehder et Wilson and *Sinowilsonia henryi* Hemsley these bundles curve over the base of the seed and extend apically on both sides of the seed. The strap-like ridge on the internal seed molds of *Fortunearites* (Pl. 14, figs. 10–13), representing the raphe, conforms to the morphology in *Fortunearia* and *Sinowilsonia*. These two genera have been recognized as sister taxa on the basis of other characters and are placed with the more distantly related *Eustigma* in the subtribe Eustigmateae Harms (Endress, 1989a, c).

Compact globose staminate inflorescences with hamamelidaceous pollen have also been recovered from the Nut Beds (Pl. 14, figs. 14–16, Pl. 15, figs. 1–5). These inflorescences are apparently unisexual with flowers having a pair of pistilodes, a whorl of ten stamens and staminodia, five narrow petals and five sepals with a dense covering of stellate trichomes (Pl. 14, fig. 16). Only two specimens have been recovered (UF 5567, 6109). Since they appear to belong to the Hamamelidoideae, it is possible that these inflorescences also belong to *Fortunearites*. The flowers share with *Fortunearia* and *Sinowilsonia* the presence of narrow petals, and conspicuously introrse anthers. On the other hand, they differ from those of extant *Fortunearia* and *Sinowilsonia* in having ten stamens + staminodes per flower (Pl. 14, fig. 15) rather than five. Pollen from the stamens of the fossil (Pl. 15, figs. 1–5) is more similar to that of other genera such as *Hamamelis* and *Corylopsis* than to that of extant *Fortunearia* and *Sinowilsonia* (Bogle and Philbrick, 1980). If these inflorescences indeed belong to the same species as the infructescence, then the case for treating *Fortunearites* as an extinct genus is strengthened.

Family **HYDRANGEACEAE** Dumort.

The Hydrangeaceae include 17 extant genera and about 170 species of trees, shrubs, lianas and herbs, predominately temperate and distributed mostly in the northern hemisphere. Morphological, chemical and chloroplast DNA (rbcL) characters indicate that Hydrangeaceae are closely allied to the Cornaceae (Morgan and Soltis, 1993; Xiang et al., 1993). The family is represented in the Tertiary of Europe by fruits of *Dichroa*, *Hydrangea*, *Schizophraqma* and *Itea* (Mai, 1985). The showy, usually tetrasepalous, sterile flowers of *Hydrangea* are easily identified (Pl. 15, figs. 6, 9) and have been recognized from many Tertiary localities in western North America.

Genus **HYDRANGEA** L.

Hydrangea knowltonii sp. nov.

Plate 15, figures 7, 8; Plate 16, figures 1–15;
Text-figure 12

Etymology.—This species is named after the late Frank H. Knowlton, who was the first to recognize flowers of this genus in the Tertiary of North America.

Description.—Infructescence a compound, trichotomously branching dichasium at least 43 mm long; pedicels 1.5–2.7 mm long; fruits bicarpellate and tricarpellate obovoid to subconical capsules. Fruit dimensions from compression specimens: length 1.2–2.0 mm, width 1.5–2.2 mm; base acute, apex truncate with an epigynous disk; exterior of fruit with about ten longitudinal ribs; styles two to three, persistent, free, 0.6–0.8 mm long.

Silicified fruits bicarpellate and tricarpellate multiseeded thin-walled capsules, prolate, two- to three-lobed and correspondingly bi- and trisymmetrical; locule casts rounded apically and basally, height 2.4–4.0, avg. 3.3 mm (SD=0.44, n=20), maximum width in bilobed specimens 3.2–4.2, avg. 3.8 mm (SD=0.34, n=13), maximum width in trilobed specimens 3.2–4.5, avg. 4.1 mm (SD=0.53, n=5), width of individual lobes 2.3–3.8, avg. 3.1 mm (SD=0.41, n=15); endocarp wall about 45 μm thick, composed of transversely aligned fibers; apical end of the locule cast with a characteristic two- or three-angled wedge (silica-filled dehiscence opening) at the intersection of the two or three carpels; fruit unilocular, placentation deeply intruded parietal, almost axile, septa 90 μm thick, bifurcating near the center of fruit and producing a placenta from each arm. Seeds numerous, tiny, winged, 625 μm wide, 225–270 μm thick and 900 or more μm long, with a peg-like hilum and a flattened, elliptical central body, encircled longitudinally by a wing; seed coat uniseriate, made up of rectangular cells 33–58 μm in diameter, drawn out laterally into a flange that forms the wing (typically 180 μm wide); embryo straight to sinuous.

Specimens.—Holotype: UF 6445, locule cast. Paratypes: OMSI Pb475, Pb697, infructescence compressions; UCMP 10668, 10669, UF 6444, 6446, 8691–8699, 9384, 9385, 9423, 9883, USNM 312763 (Bones, 1979, pl. 6, fig. 11), 312764 (Bones, 1979, pl. 6, fig. 12), 355390, 355464 (3 specimens), 355651 (2 specimens) 355652 (13 specimens), 355658, locule casts.

Discussion.—*Hydrangea* is represented in the Nut Beds by a few compression specimens from the leaf horizon at the base of Face 3 and by many isolated chalcedony locule casts from the upper part of Face 3. The affinities of the compression fossils are readily apparent because the trichotomous mode of branching of the infructescences (Pl. 15, fig. 7) and the morphology of the fruits with their longitudinal ribbing, epigynous disk, and persistent styles (Pl. 15, fig. 8) precisely match the extant genus (Pl. 15, fig. 9).

The isolated silicified fruits were more difficult to identify at first because surface details, including the disk and persistent styles, are not preserved. Instead, the specimens are preserved mainly as locule casts with only occasional details of the fruit wall remaining. The distinctive, transversely striate locule casts vary from two- to three-lobed, i.e., two to three-carpellate and have a conspicuous two- to three-armed apical "wedge" (Pl. 16, figs. 1, 3, 6) representing the dehiscence opening. Five tricarpellate (e.g., Pl. 16, figs. 1, 2) and 17 bicarpellate specimens (e.g., Pl. 16, figs. 3, 4) were observed. In addition, numerous specimens are represented by detached unicarpellate lobes of the locule cast, broken in the process of collecting. Although the fruit wall itself is usually not preserved, striations on the locule casts (Pl. 16, figs. 1–7, 9) indicate that the surrounding endocarp was composed of transversely oriented fibers. The pericarp is partially preserved in one specimen (Pl. 16, fig. 9) showing that the thin endocarp is surrounded by a mesocarp composed mostly of isodiametric cells but with widely spaced longitudinally oriented bands of fibers. The longitudinal fiber bands of the outer layer in the silicified specimen correspond to those readily observed on the impression specimens (Pl. 15, fig. 8).

Due to the translucency of the chalcedony locule casts, seeds can sometimes be observed within them as tiny dark spots. Microscopic details of individual seeds may be observed both in thin sections of the fruits (Pl. 16, figs. 12, 13) and in preparations made by dissolving the fruits in hydrofluoric acid (Pl. 16, figs. 14, 15). The seeds have a thick, peg-like hilum and are winged. Serial transverse sections of the silicified specimens show that the seeds were borne on deeply intruded placentae (Pl. 16, figs. 8, 10, 11), as illustrated in Text-fig. 12.

In fruit shape and size, apical dehiscence, wall anatomy, placentation, seed morphology, and in the variability between two- and three-carpellate fruits, these specimens correspond precisely to extant *Hydrangea*. In her monograph of the genus, McClintock (1957) noted that variations in seed morphology (seeds caudate or not, winged or not) are of systematic utility. Seeds with a circular wing surrounding the entire seed body are confined to *Hydrangea*, section *Hydrangea*, subsection *Calyptranthe* (Maxim.) McClintock, which has a single modern species, *H. anamola* D. Don, a widely distributed species extending from eastern Himalyaya of northern India to Korea and Japan (Pl. 16, fig. 16).

Hydrangea is also known from other localities of the Clarno Formation (West Branch Creek, White Cliffs, Gonser Road) on the basis of conspicuous tetrasepalous sterile flowers (Pl. 15, fig. 6) as well as by fruiting dichasia similar to that described above. Today, *Hydrangea* includes about 23 modern species that are distributed from the Himalayas to Japan and Malesia, eastern North America, northern Central America and western South America.

Family **ICACINACEAE** Miers

The Icacinaceae are a family of trees, shrubs and lianas, mostly of tropical distribution, with about 60 extant genera and 320 species. Fruits typically are unilocular, single-seeded drupes. The family is traditionally divided into four tribes (Engler, 1897, 1964): the Icacineae (mostly trees, shrubs, seldom climbers, vessel perforations typically scalariform), the Iodeae (lianas with dioeceous flowers and vessels with simple perforations), the Sarcostigmateae (lianas, fruit locule weakly wrinkled) and the Phytocreneae (lianas, fruit locule warty or spiny). The general validity of these tribes was supported by studies of vegetative anatomy (Bailey and Howard, 1941; Howard, 1942), although there is need for refinement. The family is common in the early Tertiary of western North America, Europe and Asia, as reviewed by Tanai (1990). The family is represented in the Nut Beds by five genera and eight species: *Comicilabium*, *Iodes* (two spp.), *Iodicarpa* (two spp.), *Palaeophytocrene* (two spp.), *Pyrenacantha*. These genera belong to the tribes Iodeae and Phytocreneae, and thus probably represent lianas.

Tribe **IODEAE** Engler

Genus **IODES** Blume

Iodes multireticulata Reid et Chandler

Plate 17, figures 1–8

Description.—Endocarp bilaterally symmetrical, unilocular, single-seeded, broadly oval or ovate, laterally compressed in the plane of symmetry, lenticular in transverse section, pointed apically, rounded basally; length 3.5–4.7, avg. 4.0 mm (SD = 0.51, n = 4), width 6.4–8.0, avg. 7.1 mm (SD = 0.66, n = 4), thickness 8.0–10.0, avg. 9.3 mm (SD = 0.96, n = 4); exterior of endocarp with reticulate pattern of sharp ridges that delimit numerous shallow polygonal depressions, giving the appearance of areolate venation with occasional simple freely ending veinlets; with a keel surrounding the fruit in the plane of symmetry, this keel thicker on one of the lateral margins than on the other, containing the funicular canal which runs from the base to the apex; endocarp wall 450 μm thick, formed of dense sclerenchyma (details of cell shape not known). Locule cast similar in shape to the endocarp, but without sharp ridges, having 40–50 shallow depressions on each side, corresponding to the reticulations of the endocarp; length 6.0–11.7, avg. 7.6 mm (SD=1.7, n=11), width 4.5–9.7, avg. 6.1 mm (SD=1.42, n=11), thickness 1.2–4.4, avg. 2.8 mm (SD=0.88, n=10); locule cast surface dotted with closely and regularly spaced fine punctae (15–21 μm in diameter), about 12–16 per square mm; seed anatropous, pendulous, with apical hilum, basal circular chalaza (0.8–1.0 mm in diameter) and the raphe running longitudinally across one lateral face; surface of seed coat composed of rows of square to rectangular cells, 20–30 μm in diameter.

Specimens.—UCMP 10702, endocarp cast; UF 6458, USNM 446053, endocarp mold and locule cast; OMSI Pb180, UCMP 10714, UF 8592–8595, 9805, USNM 354779, 354781, 355034, 355526, 422394, 424647, locule casts; HU 59974, one endocarp valve. Holotype: BM v22589, locule cast from the London Clay.

Discussion.—This species is represented in the Nut Beds collections primarily by chalcedony locule casts, which are readily recognized by their faceted surfaces (Pl. 17, fig. 5). Close examination reveals regularly spaced fine punctae on the surface (Pl. 17, figs. 7, 8), indicating that the inner lining of the endocarp was papillate, as in extant *Iodes* (e.g., *I. cirrhosa,* Pl. 19, fig. 18). The endocarp itself is usually not preserved, but is represented by a space in the rock between the locule cast and the sedimentary mold of the endocarp exterior. The conspicuous reticulate sculpture of the endocarp surface may be seen on the surface of rare endocarp casts (Pl. 17, figs. 1, 2) and as an impression in the sedimentary molds of the endocarp (Pl. 17, figs. 3, 4). In some of the locule casts, a thin layer of chalcedony has fractured away to expose cells of the seed coat, and in some cases morphological features of the seed, including the hilum, raphe and chalaza, are readily apparent on the locule cast surface (Pl. 17, fig. 5).

The Nut Beds specimens conform closely in all details of their preservation to the fossils designated *Iodes multireticulata* Reid et Chandler (1933) from the London Clay flora (Reid and Chandler 1933), and I have found no morphological or anatomical features to distinguish them as a separate species. Papillae lining the locule are reported by Reid and Chandler to be 0.05 mm in diameter, whereas those on the Clarno specimens measure 0.16 to 0.21 mm. This difference may be attributed to measurements being taken from near the apex, rather than at the basal neck of the balloon-like papillae.

Placement of this species in the Icacinaceae is justified by many features including the bilaterally symmetrical, unilocular fruits, marginal funicular canal, and the raphe running along one of the flattened faces (Reid and Chandler, 1933). Assignment to the tribe Iodeae is supported by the combination of reticulate endocarp sculpture and papillate locule lining. The fossil endocarps are somewhat smaller than endocarps of the living species of *Iodes* that I have examined. Other genera with similar endocarps that are faceted and have papillate locules include *Hosiea* Hemsley and E. Wilson, with two species in China and Japan (see Mai and Walther, 1978; Mai, 1987 for fossil reports), and *Natsiatum* Buch.-Ham. ex Arn. with one species from eastern Himalaya to southeast Asia. Chandler (1962) attributed an Eocene British species to *Natsiatum* on the basis of comparison with *N. sinense* Oliv.; however, this extant species is now treated as *Hosiea sinensis* (Oliv.) Hemsl., and Chandler's species was subsequently placed in *Hosiea* (Takhtajan, 1966; Mai and Walther, 1978).

Seeking characters by which to distinguish the endocarps of *Hosiea* and *Natsiatum* from those of *Iodes*, I examined specimens of *Hosiea japonica*, *H. sinensis* and *Natsiatum herpeticum* Ham. at the US National and Harvard herbaria. Transverse fractures revealed that endocarps of each species have a papillate locule lining like that of *Iodes*, but lack a funicular canal within the endocarp (presumably this runs along the outside of the endocarp). By contrast, transverse sections of *Iodes* endocarps clearly showed the funicular canal within the endocarp along one of the lateral margins in the plane of symmetry. Although the preservation of the fossil does not show the funicular position unequivocally, it is interpreted to have been within the endocarp, supporting the placement in extant *Iodes*. The position of the funicle in extant *Natsiatum* remains to be determined. *Iodes*, which ranges today from Indomalaya to Africa and Madagascar, is distinguished from other similar genera of the family by its opposite leaves, a condition that cannot be assessed from the isolated fossil fruits.

Iodes, and/or closely related genera, are common in the Eocene of both Europe and North America. In summarizing records from the Eocene of England, Chandler (1962) recognized about five species of *Iodes* and one species assigned to *Natsiatum,* with species distinguished on the basis of differences in overall shape, number and prominence of depressions on the locule cast surface, presence/absence of stylar horns, and the spacing and size of papillae lining the locule. Using similar criteria, Knobloch and Mai (1986) provided a morphological key to six European Tertiary fruit species assigned to *Iodes*. Subsequently, Mai (1987) recognized two species of *Hosiea* and one of *Iodes* from the Paleocene of Germany. Collinson (1988) lists *Natsiatum* among fruits from the Middle Eocene Messel flora of Germany, an example of which is figured by Schaarschmidt (1988, p. 42). Similar endocarps are preserved as impressions at other localities of the Clarno Formation and in the middle Eocene Bridger Formation of southwestern Wyoming (Blue Rim site, UF loc. 15761; S. R. Manchester, pers. obs.).

Iodes chandlerae sp. nov.
Plate 17, figures 9–16

Etymology.—This species is named in memory of Marjorie E.J. Chandler, recognizing the importance of her contributions to the study of fossil Icacinaceae and other plant families.

Description.—Locule cast more or less ovoid, bilaterally symmetrical, somewhat compressed in the plane of symmetry, elliptical in cross section; length 7.2–9.5, avg. 8.4 mm (SD=O.99, n=8), width 6.2–7.2, avg. 6.9 mm (SD=0.37, n=8), thickness 4.3–5.6, avg. 5.2 mm (SD=0.59, n=8); base truncate, apex asymmetric, pointed; a keel or prominent ridge follows the plane of symmetry from base to apex; in addition a prominent ridge runs medially across the lower half of both longitudinal faces; the ridges intersect at right angles over the basal truncation; surface on some specimens faintly faceted and dotted with fine punctae. Seed one per locule, surface of seed coat composed of rows of square to rectangular cells 20–30 μm in diameter arranged in rows.

Specimens.—Holotype: USNM 424743. Paratypes: UCMP 10650, 10651, UF 9602, USNM 312760 (Bones, 1979, pl. 4, fig. 8), 355408 (3 specimens), 355486 (2 specimens), 355402, 422383, 424740–424743.

Discussion.—Locule casts of *I. chandlerae* differ from those of *I. multireticulata* by their more inflated, thicker appearance, less obvious surface depressions and truncate base. The affinities were unclear until a few specimens showing the characteristic punctae were found, indicating a fruit with a papillate locule. In one of the locule casts a layer was broken away, revealing a seed cast inside with details of the raphe and chalaza, and features of the seed coat surface (Pl. 17, figs. 9, 10). The truncate base with a cross-like pattern of four intersecting meridional ribs (Pl. 17, figs. 14–16) sometimes occurs in extant *Iodes* and is also seen in the icacinaceous fossil, *Palaeophytocrene pseudopersica* (Pl. 20, fig. 10). The distribution and size of punctae (Pl. 17, figs. 11, 12) are similar to that of *Iodes multireticulata*. Because the species is known only from chalcedony locule casts, external features of the endocarp remain unknown.

Genus **IODICARPA** gen. nov.

Etymology.—*Iodeae* (an extant tribe of Icacinaceae) + *karpos* (Gr = fruit).

Generic Diagnosis.—Endocarp ellipsoidal, bilaterally symmetrical, compressed in the plane of symmetry, length 26–56 mm, width 20–35 mm, thickness 9–21 mm, unilocular, single-seeded, endocarp two-valved with dehiscence along the plane of symmetry; funicular canal passing from base to apex through the endocarp wall on one side in the plane of symmetry; endocarp wall thick (2–4 mm), composed of interlocking digitate cells with numerous intracellular spaces; locule smooth, lined by rounded balloon-shaped papillae.

Type species.—*Iodicarpa ampla* sp. nov.

Discussion.—*Iodicarpa* is represented by two species in the Nut Beds assemblage. The fruits are easily distinguished from those of *Iodes* by their large size and thick endocarp wall, but resemble *Iodes* in general form, endocarp wall composed of digitate cells and papillate locule lining (Pl. 19, fig. 18).

It was considered that these fossils might be placed in the genus *Icacinicarya* Reid et Chandler. *Icacinicarya* was established to accommodate fossil endocarps and seeds with characters diagnostic of the family Icacinaceae, but not assignable to a particular modern genus or section (tribe) within the family (Reid and Chandler, 1933). However, the Nut Beds fossils clearly conform to the tribe Iodeae, and differ from the London Clay species of *Icacinicarya*. Of the 12 species attributed to *Icacinicarya* by Reid and Chandler (1933), *I. platycarpa* (the first species that they described) is hereby designated the type species. The locule of *I. platycarpa* is faceted, the locule lining is not papillate and the endocarp is formed of small cells "with no appearance of digitation, although some of the cells show sinuous outlines" (Reid and Chandler, 1933, p. 345). *Iodicarpa* does not appear be represented among the London Clay fossils.

Iodicarpa ampla sp. nov.
Plate 18, figures 1–6, 11

Etymology.—*Ampla* (L = large) referring to the large size of these fruits relative to those of Iodes.

Description.—Endocarp ellipsoidal, bilaterally symmetrical, compressed in the plane of symmetry, with a width/thickness ratio of about 1.6, unilocular, single-seeded, endocarp length 26–35, avg. 31 mm (SD=2.66, n=12), width 21.0–30.4, avg. 26.0 mm, (SD=3.27, n=12), thickness 10.0–17.0, avg. 13.6 mm (SD=1.98, n=12), outer surface (rarely preserved) with a network of sharp ridges defining numerous polygonal areas in a pattern resembling areolate venation; worn endocarp surface rugulate, with rugulae mostly oriented longitudinally; endocarp two-valved with plane of splitting along the plane of symmetry; funicular canal passing from base to apex through the endocarp wall on one side in the plane of symmetry; endocarp wall 4.2 mm thick, composed of three anatomical layers: the outer ⅓ made up of interlocking thick-walled anticlinally elongate cells with sinuous margins, 70–150 μm long and 50–63 μm wide; middle ⅓ composed of similar elongate sinuous-walled cells mostly oriented longitudinally; inner ⅓ composed of similar but smaller interlocking cells; locule lined by rounded balloon-shaped papillae, 20–33 μm wide, 27–33 μm long.

Specimens.—Holotype: USNM 354788, permineralized endocarp. Paratypes: OMSI Pb245, UF 8596, 8618, UM 29940, USNM 354782, 355269, 446055, 446085, endocarps; USNM 354159, 354198, 354241, 354787, 354789, 354790, 354794, 354797, 354801, 354802, 354804, 354806, 354808, 354813, 354814, 354818, 354820, 354821, locule casts.

Discussion.—This species is represented by permineralized endocarps and chalcedony locule casts. Because of the way in which the carbonized or incompletely permineralized endocarps break out of the hard matrix with part of the wall remaining attached to the mold, the outermost surface of the endocarp is only rarely visible. The reticulate ridge pattern of the true endocarp surface is best seen as an impression surface on the sedimentary mold from which a carbonized endocarp has been removed (Pl. 18, fig. 3). Transverse sections of permineralized endocarps reveal the thickness and bivalved construction of the endocarp wall and the position of the funicular canal (Pl. 18, fig. 6). Thin sections show sinuous-walled cells making up the endocarp wall and papillae lining the locule (Pl. 18, fig. 11).

This species corresponds to the Icacinaceae in the presence of two endocarp valves, one locule, one seed and with the funicle running through the thickness of the endocarp wall on one of the lateral margins, in the plane of bisymmetry (Pl. 18, fig. 6). *Iodicarpa ampla* resembles the extant genus *Iodes* in the course of the funicle, the papillate locule lining and the reticulate ridge pattern of the endocarp surface. However, the fossil fruits are much larger and have thicker walls than those of any modern species of the *Iodes*, and have a smooth, rather than faceted, locule.

Iodicarpa lenticularis sp. nov.

Plate 18, figures 7–10, 12–14

Etymology.—*Lentis* (L = lens-shaped), referring to the endocarp and locule cast morphology.

Description.—Endocarp ellipsoidal, bilaterally symmetrical, compressed in the plane of symmetry, lenticular in cross section, unilocular, single-seeded, width/thickness ratio 1.9–2.2; endocarp length 31.6–56.1, avg. 44.0 mm (SD=9.2, n=7), width 20.0–35.0, avg. 30.1 mm (SD=5.2, n=8), thickness 9.4–20.5, avg. 4.9 mm (SD=33, n=8) (smaller one, UF 9745, 24 mm long, 21.4 mm wide, 12.5 mm thick), exterior of endocarp relatively smooth; endocarp two-valved with dehiscence along the plane of symmetry; funicular strand running in a conspicuous canal along a lateral margin of the endocarp within the wall; endocarp wall 2.0–2.5 mm thick, composed of three anatomical layers: the outer ⅓ composed of interlocking thick walled anticlinally elongate cells with sinuous margins, 60–220, avg. 130 μm long and 30–65, avg. 45 μm wide; middle ⅓ composed of similar elongate sinuous cells mostly oriented longitudinally; inner ⅓ composed of smaller isodiametric cells, 10–15, avg. 13 μm in diameter; locule lined by rounded balloon-shaped papillae, 18–25, avg. 21 μm wide, 18–30, avg. 20 μm long; seed coat uniseriate, composed of thin walled polygonal cells, 15–25, avg. 20 μm in diameter.

Specimens.—Holotype: USNM 354816, permineralized endocarp. Paratypes: UF 8585–8591, 8614, 8615, 8616, 9745, UM 29943, USNM 354816, 354796, 354833, 354834, 354842, 354850, 354979, 354985, endocarps; USNM 354793, 354795, 354852, locule casts.

Discussion.—A locule cast of this species was illustrated by Scott (1954, pl. 16, fig. 31), but not named; only one specimen was known at that time. Specimens are preserved variously as isolated chalcedony locule casts, individual endocarp valve casts, and as complete carbonized or permineralized endocarps. Sections of permineralized endocarps reveal that the wall is composed of elongate cells with sinuous walls and show the conspicuously papillate locule lining (Pl. 18, figs. 12–14). These anatomical features, along with the two-valved, unilocular, single-seeded endocarps, confirm the position of this species as a member of the Icacinaceae.

Anatomically, the endocarp of *Iodicarpa lenticularis* is virtually identical to that of *I. amplum*. However, *I. lenticularis* is readily distinguished by its greater length and commonly more compressed form, giving a greater width to thickness ratio, and by its smooth, rather than sculptured, endocarp surface.

Genus **Comicilabium** gen. nov.

Etymology.—*Comicus* (L = funny) + *labium* (L = lip), referring to the shape of the funicular bulge.

Type species.—*Comicilabium atkinsii* sp. nov.

Comicilabium atkinsii sp. nov.

Plate 19, figures 1–9

Etymology.—This species is named for Alexander Atkins, in recognition of his invaluable assistance with field work at the Nut beds.

Description.—Endocarp subglobose, bilaterally symmetrical, unilocular, single-seeded, somewhat compressed in the plane of symmetry; length 18.2–30.2, avg. 29.0 mm (SD=8.49, n=7); width 24.0–42.4, avg. 30.9 mm (SD=7.02, n=7); thickness 21.0–30.2, avg. 25.0 mm (SD=3.35, n=6); with about five faint longitudinal grooves on both faces, radiating from a point at the base and extending toward the apical bulge; a fine groove running along the surface in the plane of bisymmetry disappearing over the apical bulge; apical bulge forming a conspicuous lip with a transverse slit 8–9 mm wide perpendicular to the plane of bisymmetry; funicular canal running longitudinally within the endocarp wall in the plane of symmetry on one side, turning inward at the apical bulge; endocarp wall 2–4 mm thick with a compact structure made up interlocking (jig-saw puzzle-like) digitate cells; cells of the outer part elongated with long axes anticlinal, 25–100 μm in diameter; those of the inner part of the endocarp elongate with long axes horizontal/periclinal, 10–12 μm in diameter, typically 75 μm long; locule lined by short bubble-like papillae 12–15 μm in diameter; locule cast smooth, rounded basally, tapering to a point apically, with a keel along one side in the plane of symmetry.

Specimens.—Holotype: USNM 354783. Paratypes: UF 8596, OMSI Pb245, UM 29941, 66136, USNM 354782, 355269, 446055, 446084, endocarps; USNM 354159, 354198, 354241, 354787, 354790, 354794, 354797, 354801, 354802, 354804–354806, 354808, 354813, 354814, 354818, 354820, 354821, locule casts.

Discussion.—This species is represented by endocarp casts, permineralized endocarps, and locule casts. It is conspicuous by the prominent apical placental bulge where the funicle curves into the locule (Pl. 19, figs. 1, 2, 5), and by the longitudinally oriented grooves on the endocarp surface. A surface groove in the plane of bisymmetry (Pl. 19, figs. 2–4) indicates that the fruits were two-valved. Sectioned permineralized endocarps reveal a thick endocarp wall (Pl. 19, figs. 7, 8), a single seed with paired subplanar cotyledons (Pl. 19, fig. 7), and papillae lining the locule (Pl. 19, fig. 9).

The combination of a unilocular endocarp, having the funicle on one side in the plane of symmetry, interlocking digitate cells and papillate locule lining confirms affinities with the Icacinaceae. The papillate locule lining is a condition found sporadically in the tribes Iodeae and Phytocrenae, and is seen in other icacinaceous genera from the Nut Beds including *Iodes* (Pl. 17, fig. 8), *Iodicarpa* (Pl. 18, figs. 12, 14), and *Palaeophytocrene* (Pl. 20, fig. 5). Because I have not found a modern genus with precisely corresponding morphology, I conclude that this species represents and extinct genus, for which the name *Comicilabium* is established. *Comicilabium* differs from *Iodicarpa* by the large funicular bulge, the straight meridional furrows, and its greater thickness measured across the plane of symmetry. In addition, *Comicilabium atkinsii* differs from the Clarno species of *Iodicarpa* in having larger, shorter papillae.

Tribe **PHYTOCRENEAE** Engler

Genus **PALAEOPHYTOCRENE** Reid et Chandler

The genus *Palaeophytocrene* was established by Reid and Chandler (1933) to accommodate fossil fruits with tuberculate endocarps similar to those occurring in the extant tribe Phytocreneae of the Icacinaceae. These fossils are easily recognized by the prominent pits (tubercles) on the surface of endocarps and locule casts, and are relatively common in the Nut Beds (Scott, 1954). In the distribution and nature of tubercles on the surface of the endocarp, the fossil genus resembles modern *Phytocrene* Wall (Pl. 19, fig. 16). As Reid and Chandler (1933) observed, however, the tubercles of *Palaeophytocrene* extend well into the locule whereas those of *Phytocrene* protrude only slighty, if at all, into the locule (Pl. 19, fig. 17). Other extant genera with tuberculate endocarps include *Miquelia* Meissn., *Chlamydocarya* Baill., and *Pyrenacantha* Hook. These genera occur today in the Old World tropics. Detailed anatomical studies of extant fruits of the Phytocreneae have not been published, aside from the observations of Reid and Chandler (1933), and the functional significance of the tubercles (or "canals", Scott, 1954) remains unknown. In contrast to *Iodes*, *Comicilabium*, and the *Iodicarpa* species treated above, *Palaeophytocrene*, *Phytocrene* and *Pyrenacantha* do not show a funicle in cross sections of the endocarp.

Palaeophytocrene is now known from many Paleogene localities in the northern hemisphere, including the Paleocene of North Dakota and Wyoming (Crane et al., 1990), the early Eocene Chalk Bluffs flora of California (MacGinitie, 1969, p. 132), the middle Eocene of Messel, Germany (Collinson, 1988), Republic Washington (W. Wehr, pers. comm.), and Bonanza, Utah (S. R. Manchester, pers. obs.), the Oligocene Gray

Butte, (M. A. Ashwill, pers. comm.), Dugout Gulch and Willamette (S. R. Manchester, pers. obs.) floras of Oregon, as well as from the London Clay flora (Reid and Chandler, 1933; Collinson, 1983).

Scott (1954) recognized three species of *Palaeophytocrene* from the Nut Beds: *P. foveolata* Reid et Chandler, *P. pseudopersica* Scott and *P. hancockii* Scott, based upon six, three and one specimens, respectively. A much larger collection of *Palaeophytocrene* endocarps and locule casts is now available, leading to a revised interpretation of this complex. I adopt only two of Scott's *Palaeophytocrene* species for the Nut Beds material: *P. hancockii* and *P. pseudopersica*. Of the three specimens attributed by Scott (1954) to the London Clay species *P. foveolata* Reid et Chandler, one (his pl. 16, fig. 3) is treated here as *Palaeophytocrene pseudopersica*, and two (pl. 16, figs. 1, 2) belong to *Pyrenacantha occidentalis* sp. nov.

Palaeophytocrene hancockii Scott emend.
Plate 20, figures 1–5

Palaeophytocrene hancockii Scott 1954, p. 81, pl. 16, figs. 6, 7.

Description.—Endocarp large, ovoid, bilaterally symmetrical, unilocular, single-seeded, somewhat compressed in the plane of symmetry, length 38.5–85.0, avg. 64.6 mm (SD=12.64, n=12), width 26.9–50.0, avg. 37.2 mm (SD=6.53, n=11), thickness 20.0–35.0, avg. 28.4 mm (SD=4.56, n=9); outer surface covered by numerous pits, about 9 rows wide and 13–14 high, adjacent pits sometimes coalesced; endocarp wall 2.0–2.3 mm thick, composed of densely packed interlocking digitate cells, up to 200 μm long and 30–80 μm wide, arranged in layers parallel to the locule surface; tubercles (corresponding to the surface pits) about 2.2 mm in diameter, protruding 2.0–3.5 mm into the locule, straight-walled (cylindrical, sometimes bulbous-ended); locule finely papillate, papillae 10–15 μm high and wide; funicle not present in the endocarp.

Specimens.—Holotype: UM 29933 (Scott, 1954, pl. 16, figs. 6, 7). Hypotypes: USNM 312751 (Bones, 1979, pl. 4, fig. 6), UCMP 10715, 10716, UF 8603, 8604, 8612, 9567, USNM 354420, 354155.

Discussion.—*Palaeophytocrene hancockii* includes the largest of all fruits known from the Nut Beds. Scott (1954) distinguished this species from other species of *Palaeophytocrene* on the basis of its large size, and because, in proportion to its size, the tubercles protrude only a short distance into the locule by comparison with the other species of this genus. His description was based on a single specimen that had been sectioned transversely to show the endocarp wall, but in which the number and arrangement of pits are obscured. There are about 15 specimens now, including specimens that clearly show the number and arrangement of pits (Pl. 20, figs. 1, 2). Thin sections show the structure of the tubercles projecting into the locule (Pl. 20, figs. 3, 4), and the anatomy of the endocarp wall, including papillae lining the locule (Pl. 20, fig. 5).

Palaeophytocrene pseudopersica Scott emend.
Plate 20, figures 6–13

Palaeophytocrene pseudopersica Scott 1954, p. 80, pl. 16, figs. 4, 5.
Palaeophytocrene foveolata Reid and Chandler. Scott 1954, pl. 16, fig. 3 only.

Description.—Endocarp unilocular, single-seeded, oval to ovate, flattened or slightly inflated in the plane of bisymmetry, length 14.3–39.0, avg. 27.4 mm (SD=7.8, n=8), width 13.0–28.5, avg. 21.4 mm (SD=5.3, n=8), thickness 8.8–16.5, avg. 10.9 mm (SD=2.6, n=8); outer surface covered by numerous pits, eight to 14 pits wide, ca. 19 pits high (ca. 40–80 pits on each half of the endocarp), adjacent pits sometimes coalesced; endocarp wall 1.5–2.3 mm thick, composed of densely packed interlocking digitate cells; these cells up to 300 μm long and 20–50 μm wide, oriented in layers parallel to the locule surface; hollow tubercles (corresponding to the surface pits) 1.2–2.4 mm in diameter, protruding 1.7–3.1, avg. 2.2 mm into the locule, straight-walled (cylindrical), sometimes conical; locule lining, including that over the tubercles, finely papillate; papillae short, rounded 10–15 μm high and wide, closely spaced. Seed not seen, but possible fragments of very thin seed coat observed in sectioned specimens.

Specimens.—Holotype: UM 29931. Hypotypes: OMSI Pb178, Pb179, Pb181, Pb182, Pb247, UF 8597, 8599, 8602, 8605–8610, 8613, 9568, 9569, UM 29928, 29929, 29931, 29932.

Discussion.—Scott (1954) described this species to accommodate Clarno fossils that he noted were similar to the London Clay species, *P. ambigua* Reid and Chandler. The species is represented by abundant locule casts (Pl. 20, figs. 12, 13) and permineralized endocarps (Pl. 20, figs. 6–10) that range widely in size. The above description incorporates new anatomical data observed in thin sections (e.g., Pl. 20, fig. 11).

As far as I can determine, there is not a very clear distinction between *P. pseudopersica* and *P. hancockii*, and the practice has simply been to place large specimens (38–85 mm long) in *P. hancockii* and smaller specimens, usually less than 40 mm long, in *P. pseudopersica*. The variation in size among specimens of *Palaeophytocrene* from the Nut beds is great. I excluded two of the smallest specimens from the above description (UF 8609, 8610, which are 7.8, 11.8 mm long, 7.0, 9.0 mm wide, and 5.0, 6.0 mm thick), because they might be immature, or could represent another species. The variation is more or less continuous, however, and, if more than one species is represented, it is difficult to draw distinct boundaries between them. Scott noted that in proportion to its size, the tubercles of *P. hancockii* protrude only a short distance into the locule in comparison with *P. pseudopersica*. However, the same phenomenon is noted in comparing successively larger specimens of *P. pseudopersica*. Evidently, the projections do not increase in thickness in direct proportion with increased fruit size in this genus. I have chosen to maintain two of the species established by Scott (1954), while recognizing that the large collections of this genus require more thorough investigation to determine the number of species represented. In order to understand better the significance of the size variability among *Palaeophytocrene* specimens from the Nut Beds, it would be desirable to obtain information on the intraspecific and ontogenetic size variability among related extant genera such as *Miquelia*, *Chlamydocarya* and *Pyrenacantha*.

Genus **PYRENACANTHA** Hooker

Pyrenacantha occidentalis sp. nov.
Plate 19, figures 10–14

Palaeophytocrene foveolata Reid et Chandler. Scott 1954, pl. 16, fig. 1, only.

Etymology.—*Occidens* (L = of the west) referring to the western occurrence of this species, which contrasts with the distribution of extant species in the eastern hemisphere.

Description.—Endocarp ovoid, bilaterally symmetrical, slightly compressed in the plane of symmetry, unilocular, single-seeded; length 25.0–33.0, avg. 29.9 mm (SD=2.53, n=8), width 15.7–30.0, avg. 22.7 mm (SD=4.18, n=7), thickness 11.0–25.3, avg. 18.3 mm (SD=4.32, n=7), surface dotted with numerous small pits about 1 mm in diameter, spaced 1–2 mm apart, 12–14 rows of pits wide, 16–19 pits high; pits corresponding to elongate vertical-sided, cylindrical, tubercles which project 4.5–5.2 mm into the locule (protruding more than ⅓ of the distance across the locule), endocarp wall 1.0 mm thick, uniform, without funicular canal; cells of the endocarp elongate, sinuous. Locule lining not papillate, seed conforming to the locule projections.

Specimens.—Holotype: UCMP 10708. Paratypes: OMSI Pb170, Pb202, UCMP 10706, UF 8617, UM 29927 (Scott, 1954, pl. 16, fig. 1), USNM 354767, 354987 (and another portion of the same specimen, 354989).

Discussion.—Endocarps of this species differ from those of *Palaeophytocrene* by having much longer protrusions into the locule, and by the thinner endocarp wall (Pl. 19, figs. 12, 13). There is a very close resemblance to endocarps of *Pyrenacantha zenkeri* (Sp. Moore) Exell from Angola, Africa, although the few specimens observed (e.g., Pl. 19, fig. 15) were smaller (only 15 mm long). Both are similar in having a thin endocarp with long protrusions into the locule. The genus *Pyrenacantha* has also been recognized in the Philippines (Sleumer, 1969). This is the first recognition of *Pyrenacantha* from the North American fossil record.

Family **JUGLANDACEAE** A. Rich ex Kunth.

The Juglandaceae (walnut family) are a family of temperate to tropical trees with eight extant genera placed in four tribes: the Juglandeae (*Juglans*, *Pterocarya*, *Cyclocarya*), Hicorieae (*Carya*), Engelhardieae (*Engelhardia*, *Oreomunnea*, *Alfaroa*), and Platycaryeae (*Platycarya*). The family has an excellent fossil record of extant and extinct genera in the Tertiary of North America, Europe and Asia (reviewed by Manchester, 1987a, 1989b). It is represented in the Nut Beds by wood of *Engelhardioxylon* (Manchester, 1983) and *Clarnoxylon* (Manchester and Wheeler, 1993) and by fruits of *Cruciptera*, *Juglans*, cf. *Palaeocarya* and *Paleoplatycarya*?, described below.

Tribe **JUGLANDEAE**

Genus **CRUCIPTERA** Manchester

Cruciptera simsonii (Brown) Manchester
Plate 21, figures 10–17

Tetrapteris simsoni Brown 1940, pp. 344–356, fig. 9.
Cruciptera simsonii (Brown) Manchester 1991, p. 719, figs. 1–11, 13–15.

Description.—Samara with four bract-wings radiating in a plane surrounding a globose nutlet; fruit width including wings 25.0–38.0, avg. 33.2 mm (SD=6.45, n=5); pedicel 0.4 mm thick, at least 5.0 mm long, aligned with the axis of symmetry; nutlet globose except for an apical stylar projection, rounded basally, smooth, length 3.4–4.5 mm, equatorial diameter 3.6–5.0, avg. 4.2 mm (SD=0.5l, n=6), nutlet unilocular; nutshell 0.2–0.3 mm thick, composed of isodiametric sclereids 15–30 μm in diameter; base of the locule divided into four lobes by thick primary and secondary septa; secondary septum oriented in the plane of carpel closure, extending about ⅓ of the distance from base to apex of the fruit; primary septum complete except for an aperture in the apical ⅓ of the nutlet; two lacunae, more or less circular in cross section, situated near the periphery of the primary septum; plane of dehiscence dividing the nutshell into two halves, aligned with the secondary septum; wings attached in a plane about the equator of the nutlet; wings narrow, elongate, spatulate to parallel-sided, bluntly rounded to pointed at the apices; wing length 11.0–17.0 mm, width 2.5–4.6, avg. 3.5 mm (SD=0.73, n=8), venation subparallel, somewhat spreading distally, without cross veins, occasionally dichotomizing, 15 to 20 veins across at the widest point of the wing, veins terminating distally without forming loops.

Specimens.—OMSI Pb776, Pb899, Pb1175, Pb1580, UF 9263, 9612, samaras; UF 8867, permineralized nutlet; USNM 354375, locule cast. Holotype: USNM 42334, a compression specimen from Clarno West Branch Creek locality.

Discussion.—*Cruciptera simsonii* occurs at several localities of the Clarno Formation, including West Branch Creek, White Cliffs, Red Gap, Alex Canyon, Gosner Road, Dry Hollow and John Day Gulch (Text-fig. 2), and is also represented by a specimen from the middle Eocene Cashman locality of the Puget Group, western Washington (USGS loc. 9731, listed as *Tetrapteris simsoni* in Wolfe, 1968). The above description is based only upon the Nut Beds specimens; features of the four sepals and two styles have been described previously based upon specimens from other Clarno localities (Manchester, 1991). Samaras with intact wings (Pl. 21, figs. 10–13) are relatively common in the basal leaf layer of Face 3, and a few isolated silicified nutlets and locule casts (Pl. 21, figs. 15–17) were found elsewhere in the locality. The silicified nutlets reveal internal structure and anatomy but do not show the wings. Conversely, the impression specimens preserve the morphology and attachment of wing and petiole, but do not show internal details of the nutlet. One important specimen, however, shows both the wings (Pl. 21, fig. 11) and a well preserved nutlet (Pl. 21, fig. 14) with the same internal structure as the isolated silicified nutlets, thus linking impression and petrifaction specimens as the same species.

Transverse sections of the nutlets reveal a well developed basal secondary septum in addition to the primary septum dividing the locule into four chambers (Pl. 21, figs. 14–16). Accordingly, the associated chalcedony locule casts are basally four-lobed (Pl. 21, fig. 17), and are readily distinguished from the other small juglandaceous locule casts that occur in the Nut Beds, i.e., the two-lobed locule casts associated with *Paleoplatycarya* (Pl. 22, figs. 5–8) and *Palaeocarya* (Pl. 22, figs. 15, 16). The morphology of the nutlets and locule casts of this species are clearly juglandaceous. The nutshell and septa are composed of isodiametric sclereids, differentiating them clearly from those of the tribe Engelhardieae which are composed of fibers. The orientation of the wings in a plane perpendicular to the nutlet axis is a feature shared with extant *Cyclocarya*, and the extinct Paleocene genus *Polyptera* (Manchester, 1989b, 1991).

Cruciptera is also known from the Early Eocene of Wyoming, the Oligocene of Oregon and from the Middle Eocene of Dorset, England ("*Abelia* sp.", Chandler, 1964) and Messel, Germany (Manchester, 1991),[3] and appears to predate the appearance of *Pterocarya* fruits (Late Eocene/Early Oligocene) in the fossil record. The foliage and pollen of *Cruciptera* remain to be determined. Juglandaceous leaflets from the Nut Beds that were described and illustrated (Manchester, 1987a, p. 89, fig. 38) as "*Juglans* (?) sp." were collected in the same stratigraphic layer as fruits of *Cruciptera* and are a candidate for the type of foliage produced by the extinct genus. Although the irregular spacing and course of secondary and tertiary veins is similar to that of extant leaflets of *Juglans* sect. *Rhysocaryon*, the shape, size, and venation of the teeth more closely resemble *Pterocarya*. *Pterocarya* fruits are absent from the entire Clarno formation; thus the foliage probably corresponds either with *Juglans* or *Cruciptera*.

Genus JUGLANS L.

Juglans clarnensis Scott

Plate 21, figures 1–9

Juglans clarnensis Scott 1954, p. 70, pl. 15 figs. 1–14; Bones 1979, pl. 2, fig. 6–8; Manchester 1987a, p. 107, fig. 46A–M.

Description.—Nut globose to ellipsoidal, circular in cross section, unilocular, single-seeded, base rounded with slight depression in the attachment area, extreme apex sometimes with a small point; length 13.4–27.1, avg. 21.6 mm (SD=2.77, n=61), equatorial diameter 15.4–23.4, avg. 19.3 mm (SD=2.01, n=65); surface with eight to 12 shallow longitudinal grooves joining at base and apex, sometimes anastomosing, including a pair of grooves corresponding to the plane of dehiscence, nutshell 2–4 mm thick; primary septum perpendicular to the plane of dehiscence with an aperture in the apical half, containing a pair of small longitudinal lacunae; secondary septum absent to rudimentary at the base of the locule in the plane of dehiscence; each valve of the nutshell containing a pair of laterally flattened longitudinal lacunae 4–8 mm wide and 1–1.5 mm thick that join together at the base and apex; vascular supply of the primary septum axial in course. Locule cast smooth, quadrilaterally symmetrical about vertical axis, rounded basally, divided by the primary septum into two major lobes at the base, which are sometimes slightly emarginate basally by the faint development of a secondary septum; apex sharply pointed, shoulder region concave to seldom convex.

---

[3] See also Notes added in proof, p. 200.

Specimens.—Syntypes: UM 29906, 29907, 29908 (Scott, 1954). Hypotypes: UF 4781, 4872, 4873, 4875, 5338, 7965, 9424–9448, USNM 312378 (Bones, 1979, pl. 2), 354282–354291, 354293–354299, 354300–354315, 354361, 354362, nuts; OMSI Pb186, 188, 189A, 237, 241, 251, UF 4874, 5339, 5340, 7965, 9437, 9440, 9451–9469, UM 29908, USNM 354245–354246, locule casts.

Discussion.—*Juglans clarnensis* is the oldest confirmed fruit record of *Juglans* (Scott, 1954; Manchester, 1987a). There are more than 200 specimens of this species in museum collections, preserved as nut casts (Pl. 21, figs. 1, 2) and molds, occasional permineralized nuts (Pl. 21, figs. 3, 4), and locule casts (Pl. 21, figs. 5–9). Many more specimens of the esteemed Clarno walnut reside in private collections. The specimens are most common in the middle and upper levels of Faces 1 and 2. Nuts that may represent the same species are preserved as silica casts at the Brummers Spring locality (Text-fig. 2; Manchester, 1990).

Criteria for placing this species in the extant genus *Juglans* were presented by Scott (1954) and Manchester (1987a). *Juglans clarnensis* possesses nutshell morphology most similar to that of section *Rhysocaryon* (black walnuts) but has a less convoluted seed morphology similar to that of to section *Cardiocaryon* (butternuts).

Tribe ENGELHARDIEAE

Genus PALAEOCARYA Saporta

cf. Palaeocarya clarnensis Manchester

Plate 22, figures 9–17

Description.—Nutlet subglobose to obovoid, unilocular, single-seeded, circular in cross section, base acute-pointed, apex obtuse-pointed; smooth, except for a single longitudinal rib preserved in a few specimens; fruit with a single incomplete septum dividing the base of the locule and seed into two rounded lobes; primary septum 0.4–0.6 mm thick, without lacunae, two vascular bundles running axially through the septum adjacent to the central axis; secondary septum absent; nutshell thin (0.25 mm), without lacunae, composed of longitudinally oriented fibers; plane of dehiscence at right angles to the primary septum. Locule cast smooth, quadrilaterally symmetrical about vertical axis, basally bilobed, each lobe corresponding to a cotyledon, rounded basally and laterally, pointed apically, length 1.5–3.8, avg. 2.3 mm (SD=0.57, n=39), width parallel to primary septum 1.7–3.4, avg. 2.6 mm (SD=0.48, n=40), width perpendicular to primary septum 1.8–3.4, avg. 2.5 mm (SD=0.45, n=38).

Specimens.—UF 9361, USNM 424640, 458416, more or less complete nutlets; HU 59994–59996, UCMP 10618–10621, UF 6456, 8747–8762, USNM 354364 (4 specimens in matrix), 354366 (15 specimens), 354367, 354368 (2 specimens), 354369 (5 specimens), 354370 (11 specimens), 354371, 354372 (7 specimens), 354374 (5 specimens), 354377 (3 specimens), 354378, 424640, 424703, locule casts.

Discussion.—This species is known from numerous chalcedony locule casts (Pl. 22, figs. 9, 15, 16) and only a few partially complete permineralized nuts (Pl. 22, figs. 10–12, 14) which in section show the thin, smooth wall of the nutshell (Pl. 22, figs. 13, 17). Specimens were found in the upper part of Faces 1 and 3 of the Nut Beds, but not in the lower levels of finer grained sediments where samaras with intact wings would be likely to preserve. The juglandaceous morphology of the locule casts is clear from a simple comparison with the larger locule casts of *Juglans clarnensis* (Pl. 21, figs. 5–9). The locule casts range greatly in size such that the smallest are about half the size of the largest, but no morphological differences were detected. Although none of the specimens have been found with remains of wings preserved, the small size is an indication that they are probably from winged fruits. The single rib remaining on some nutlets (Pl. 22, figs. 11, 14) may be a remnant of the midvein of a wing like that of *Engelhardia*.

These nutlets and locule casts probably represent the engelhardioid taxon, *Palaeocarya clarnensis*, a winged fruit common at other localities of the Clarno Formation (Manchester, 1987a). Without diagnostic characters from the wings, however, the Nut Beds material cannot be identified to *Palaeocarya* with certainty. The following lines of evidence, however, support the hypothesis that these fossils represent *P. clarnensis*: 1) We know that these were not the locule casts of *Cruciptera*, because *Cruciptera* fruits with intact nutlets show a basally four-lobed, not two-lobed, locule (cf. Pl. 21, fig. 17 with Pl. 22, fig. 9); 2) Affinities with *Platycarya* are also eliminated on the basis of locule cast morphology (cf. Pl. 22, figs. 5–8); 3) The nutlets of compressed fruits of *P. clarnensis* are highly variable in size, as are the isolated nutlets described above; 4) The nutshell and septa are composed of fibers, not sclereids, indicating affinities with the tribe Engelhardieae; 5) Wood of the Engelhardieae, the same tribe to which *Palaeocarya* belongs, is present in the Nut Beds (Manchester, 1983).

Palaeocarya is a generic name accommodating fossil fruits with characters found today both in the Asian genus *Engelhardia* and in the central American genus *Oreomunnea*. The fruits of these genera are samaroid, with a large trilobed wing developed from the inflorescence bract. If the species described above actually represents *Palaeocarya clarnensis*, then it appears that it was produced by a plant more similar to *Engelhardia* than to *Oreomunnea*. The bilobed locule casts of this species indicate a two-chambered nutlet like that of *Engelhardia* rather than an eight-chambered nutlet like that of *Oreomunnea*.

Tribe PLATYCARYEAE

Genus PALEOPLATYCARYA Manchester?

Paleoplatycarya? hickeyi sp. nov.

Plate 22, figures 1–8

Etymology.—This species is named for Leo J. Hickey in recognition of his contributions to angiosperm paleobotany including the fossil record of Platycaryeae.

Description.—Infructescence elongate, estimated length 26 mm, width 4.1–4.6 mm, composed of helically arranged woody bracts on a relatively stout axis; one fruit with bilobed locule cast situated on the axil of each bract; bracts woody, shallowly v-shaped in cross section, ca. four to six bracts per cycle. Locule cast quadrilaterally symmetrical about vertical axis, obcordate in face view, pointed apically, bilobed basally, laterally compressed in the plane opposite to the primary septum, length 1.6–1.8 mm, width 2.2 mm, thickness 0.7–1.0 mm, secondary septum not developed, surface faintly verrucate.

Specimens.—Holotype: UF 6454, infructescence with intact locule casts. Paratypes: UF 9251, USNM 353995, infructescence; UF 8763, USNM 354376, 435117, locule casts.

Discussion.—This species is represented by two cone-like infructescences (Pl. 22, figs. 1–3) and a few isolated locule casts (e.g., Pl. 22, fig. 6). The juglandaceous affinity of the infructescences was not obvious until one of them was fractured to reveal the distinctive locule casts (Pl. 22, figs. 4, 5, 7, 8). The locule casts have the characteristic morphology of Juglandaceae, but are unusual in being strongly compressed in the plane perpendicular to the primary septum. This lateral flattening may have been adaptive in the context of a wind-dispersed fruit.

This species clearly belongs to the juglandaceous tribe Platycaryeae because of the cone-like infructescence with primary bracts persisting on the inflorescence axis. In all other tribes of the family, the primary inflorescence bract becomes part of the fruit and does not persist on the infructescence axis. Although the Platycaryeae have only a single modern genus, *Platycarya* of eastern Asia, the tribe was more diverse and widespread in the Tertiary, as documented by fruits, foliage and pollen from Europe and North America (Wing and Hickey, 1984; Manchester, 1987a, 1989b). The shallow v-shape of the bracts in cross section (Pl. 22, fig. 1) resembles that seen in the Eocene *Platycarya richardsonii* (Bowerbank) Chandler (cf., Manchester, 1987a, fig. 10H, I). The Nut Beds infructescence differs, however, from modern and fossil *Platycarya* species by its elongate, narrow construction.

Similarly narrow, elongate infructescences with short bracts characterize *Paleoplatycarya wingii* from the early Eocene of Wyoming (Manchester, 1987a; *Platycarya castaneopsis* sensu Wing and Hickey, 1984). However, features of the fruit wings and perianth considered diagnostic of *Paleoplatycarya* (Manchester, 1987a) are not preserved in the Nut Beds material, and no isolated fruits of *Paleoplatycarya* are known from the Clarno Formation. Pending the recovery of more informative specimens, it seems appropriate to assign this species to "*Paleoplatycarya*?".

Among extensive collections from other Clarno localities, I have observed only two other infructescences that appear to represent *P.*? *hickeyi*. Both are impression specimens from West Branch Creek (UF 9871, 9872). Another type of infructescence that is relatively common at West Branch Creek, named *Platycarya manchesteri* by Wing and Hickey (1984), is superficially similar to that described above. However, analysis of numerous specimens of *P. manchesteri* has shown that each nutlet is surrounded by four bract-like structures, rather than just one, indicating that the affinities are not with *Platycarya*. The arrangement of the bract-like structures suggests that they may be immature infructescences of *Cruciptera*.

It is possible that *P*?. *hickeyi* infructescences produced fruits of the extinct platycaryoid genus *Hooleya*. Although the distinctive biwinged fruits of *Hooleya lata* Wing and Hickey (1984) occur at the West Branch Creek and White Cliffs localities of the Clarno Formation (Text-fig. 2), they have not been identified from the Nut Beds. Locule casts of *P.*? *hickeyi* are comparable in size and shape, however, to the nutlet body seen in the compressed *Hooleya* fruits (cf., Manchester, 1987, figs. 12A–E, G, H). *Clarnoxylon*, an extinct type of juglandaceous wood known both from the Nut Beds and from West Branch Creek, possesses crystaliferous idioblasts characteristic of Platycaryeae (Manchester and Wheeler, 1993), and is a likely candidate for the type of xylem produced by *Hooleya* and/or *Paleoplatycarya* trees.

Family LAURACEAE Juss.

The Lauraceae are a family of about 45 genera and 2200 species concentrated in the tropics and warm temperate areas. The family is first reliably reported from the Cretaceous (Drinnan et al., 1990; Herendeen, 1991) and was widespread by the early Tertiary. The Lauraceae are represented in the Nut Beds by at least two types of foliage, and wood of *Ulminium* (Scott and Wheeler, 1982), as well as by the fruits described below.

Fruits of Lauraceae are unilocular and single-seeded and the seed is exalbuminous with a pair of large hemispherical cotyledons. Reid and Chandler (1933) provide an excellent synopsis of the fruit and seed characters of extant Lauraceae. The fruit may or may not be enclosed partially or completely in the hypanthium or "cupule." A prominent scar may remain at the base of the epicarp where it detaches from such a cupule. The endocarp typically has a uniseriate layer of anticlinally oriented columnar cells. This layer, which may be thick, thin or intermittent, generally appears to form the innermost coat of the pericarp. Oil cells, a feature of xylem and other tissues of Lauraceae, may also be present in the cupule and pericarp. The parenchyma or sclerenchyma cells are often oriented radially around oil cells, forming the "stellate clusters of cells" referred to by Reid and Chandler (1933) as a diagnostic feature of the family.

Although it is fairly easy to identify fruits to the Lauraceae, this family is notoriously difficult when it comes to making generic assignments. Part of the difficulty, which applies even to extant species, is that "As a rule, both floral and fruit characters are necessary for identification, but a single specimen rarely has both flowers and fruits" (van der Werff, 1991). Therefore, with the exception of *Lindera*, the Nut Beds species have been assigned to the stereotypic genera *Laurocalyx* and *Laurocarpum*.

Genus **LINDERA** Thunb.

Lindera clarnensis sp. nov.
Plate 23, figures 1–8

Etymology.—The epithet indicates the source of the species, the Clarno Formation.

Description.—Endocarp spheroidal, bilaterally symmetrical, with a faint ridge running from apex half way to base in plane of symmetry; unilocular, single-seeded; length 3.8–6.0, avg. 5.2 mm (SD=0.83, n=5), equatorial diameter 3.8–6.3, avg. 5.3 mm (SD=0.98, n=5); endocarp thin-walled, composed of a uniseriate layer of columnar cells, these cells about 100 μm high and about 15 μm wide. Seed exalbuminous, filled completely by a pair of large hemispherical cotyledons.

Specimens.—Holotype: USNM 435006. Paratypes: USNM 335472, 435007, 435008, 424728.

Discussion.—The combination of unilocular, globose endocarps (Pl. 23, figs. 1–4) with a prominent columnar layer (Pl. 23, figs. 6–8), a single seed and large plano-convex cotyledons (Pl. 23, fig. 5) confirms that this species belongs to the Lauraceae. Most extant species of Lauraceae that were examined for this study are axially elongate, rather than globose. Some extant species of *Cinnamomum* and *Lindera*, however, have small globose endocarps comparable in size and internal structure to the fossil. The endocarp wall of *Cinnamomum camphora* (L.) Presl is much thicker than that in *Lindera* spp. This fossil is virtually indistinguishable from fruits of *Lindera umbellata* Thunb. from Japan and *L. obtusiloba* Blume from the Philippines. Because of the high degree of similarity to these species, and since I have not found precisely similar species in a survey of other extant genera, the Nut Beds species is assigned to the extant genus.

Genus **LAUROCALYX** Reid et Chandler

This genus was established by Reid and Chandler (1933) for "cupuliferous fruits belonging to the family Lauraceae which, for one cause or another, cannot be referred to living genera." The preservation of a persistent perianth or cupule distinguishes this fossil genus from *Laurocarpum*.

Laurocalyx wheelerae sp. nov.
Plate 23, figures 9–15

Etymology.—This species is named for Elisabeth A. Wheeler, recognizing her contributions to the analysis of woods from the Clarno Formation, including those of the Lauraceae.

Description.—Fruit prolate, circular in transverse section, rounded apically and basally, unilocular, single-seeded, length 7.7–10.1 mm, width 7.9–10.9 mm, thickness 7.4–10.9 mm; embedded in a thick cupule covering the basal ¼ of the fruit; endocarp surface smooth, with a prominent, recessed, elliptical to reniform basal scar approximately 4.5 mm wide and 2.8 mm thick containing three vascular bundles arranged in a triangular pattern, endocarp wall about 0.7 mm thick, and composed of a uniseriate layer of anticlinally elongate cells; inside of seed with solid core of rounded parenchyma cells, 38–50 μm in diameter, this core is surrounded by larger angular parenchyma cells, to the outside of this is a uni- to biseriate seed coat of dark-pigmented periclinally elongate rectangular cells 20–22 μm high, 20–38 μm wide. Cupule composed mostly of isodiametric parenchyma cells 38–50 μm in diameter with interspersed larger cells 60–80 μm in diameter with black contents interpreted as oil cells.

Specimens.—Holotype: UF 9406. Paratypes: UF 9407–9410, USNM 355626, 355630, 355631, 355634, 355638, 435085, 424807.

Discussion.—*Laurocalyx wheelerae* is represented by permineralized fruits and locule casts, sometimes with the cupule attached. Isolated endocarps and locule casts are recognizable even without the attached cupule because of the conspicuous elliptical attachment scar (Pl.

23, figs. 9, 11). The holotype is relatively complete, including both the endocarp and the cupule. The endocarp was removed from the cupule for comparison with other isolated endocarps (Pl. 23, figs. 11, 12), and was subsequently reassembled with its cupule and sectioned longitudinally, showing the lateral extent of cupule coverage (Pl. 23, fig. 13), the presence of oil cells within the cupule (Pl. 23, fig. 14) and the layer of columnar cells in the endocarp (Pl. 23, fig. 15). These features confirm that the species represents Lauraceae.

Genus **LAUROCARPUM** Reid et Chandler

Laurocarpum Reid et Chandler is a stereotype genus erected to accommodate unilocular, single-seeded fruits that have characters diagnostic of Lauraceae, but that cannot be placed in a particular modern genus (Reid and Chandler, 1933). At least three species from the Nut Beds flora are assignable to this genus: *L. hancockii*, *L. nutbedensis*, and *L. raisinoides*, which are described below.

Scott (1954) identified one specimen from the Nut Beds to *Laurocarpum proteum* Reid et Chandler, a species based on well preserved specimens from the London Clay flora (Reid and Chandler, 1933). The specimen is an ovoid locule cast 11 mm long and 9 mm in diameter with some fragments of endocarp remaining. The shape of the apex and the truncate base with a large circular chalaza compare favorably with the London Clay species. I have reexamined the specimen figured by Scott (1954). Although external morphological features of the locule cast seem to support assignment to Lauraceae, it is unfortunate that characters of the cotyledons and wall layers remain unavailable to confirm the assignment. I have been unable to locate any additional specimens that might provide more characters upon which to confirm the systematic position of this fossil.

Laurocarpum hancockii sp. nov.
Plate 24, figures 1–3

Etymology.—The epithet is in memory of Alonzo W. Hancock, who established a field station promoting paleontological field work in the Clarno Formation.

Description.—Fruit pyriform, circular in cross section, unilocular, single-seeded, length 25 mm, equatorial diameter 18.5 mm; fruit wall 2.0 mm thick, composed of two layers: an inner uniseriate layer of anticlinally oriented columnar cells, 250 μm high and 62–112 μm wide, and an outer layer, presumably the mesocarp (exocarp not preserved), composed of a mass of thin-walled parenchyma cells 20–82 μm in diameter, arranged in radiating patterns around solitary or clustered stone cells, the stone cells or isodiametric sclereids 50–100 μm in diameter, and occasional oil cells with dark contents; seed filled by two large hemispherical cotyledons. Cupule not preserved.

Specimen.—Holotype: OMSI Pb262.

Discussion.—*Laurocarpum hancockii*, known from a single specimen, has the largest fruit of the lauraceous taxa observed from the Nut Beds. The fruit is clearly lauraceous because of the two large hemispherical cotyledons (Pl. 24, figs. 1, 2), the layer of columnar cells lining the locule (Pl. 24, fig. 3), and the presence of stone cells about which the surrounding parenchyma is stellately arranged (Pl. 24, fig. 3).

Laurocarpum nutbedensis sp. nov.
Plate 24, figures 4–7

Etymology.—The epithet nutbedensis refers to the Nut Beds locality.

Description.—Fruit prolate, unilocular, single seeded; length 8.0 mm, equatorial diameter 6.8 mm; surface relatively smooth; pericarp ca. 1.0 mm thick, consisting of: a thin uniseriate outermost layer of anticlinally oriented columnar cells 40–50 μm high, 10–15 μm wide, a main layer 750–950 μm thick composed of isodiametric parenchyma cells, typically 20–50 μm in diameter, but smaller and tangentially flattened (16–18 μm high) toward the inside of this layer, large oil cells 50–70 μm in diameter interspersed among this tissue; this layer lined on the inside by a uniseriate layer of columnar cells, and then in turn by a layer of several rows thick of rectangular cells, 200 μm thick; exocarp not preserved. Two hemispherical cotyledons filling the seed cavity.

Specimens.—Holotype: USNM 435090.

Discussion.—*Laurocarpum nutbedensis* is represented by a single permineralized specimen that has been sectioned transversely (Pl. 24, figs. 4–7). Lauraceous affinity is suggested by the columnar layers, oil cells, and single seed with hemispherical cotyledons. Oil cells of the pericarp are slightly larger and more rounded than the surrounding parenchyma cells.

Laurocarpum raisinoides sp. nov.
Plate 24, figures 8–15

Etymology.—The epithet refers to the wrinkled, raisin-like surface of the fruit.

Description.—Fruit subglobose, rounded apically and basally, unilocular, single-seeded, length 4.5 mm, equatorial diameter 4.0–5.2 mm; surface longitudinally wrinkled; pericarp with an inner uniseriate layer of columnar cells 20 μm thick giving rise to a 4–5-seriate layer of small thick walled isodiametric cells 7.5–10 μm, followed by a mesocarp layer of parenchymatous, cells 17–25 μm in diameter, with numerous interspersed oil cells 37–58 μm in diameter; exocarp uniseriate, composed of of anticlinally oriented columnar cells 21 μm high, 5 μm wide.

Specimens.—Holotype: UF 5672.

Discussion.—*Laurocarpum raisinoides* is represented by one very well preserved specimen with clear affinities to the Lauraceae. The longitudinal wrinkles on the outer surface (Pl. 24, figs. 8–10) suggest a leathery pericarp. Sections through the mesocarp reveal abundant oil cells that are larger than the surrounding parenchyma cells and filled with dark contents (Pl. 24, figs. 12–15). The endocarp and exocarp layers are composed of columnar cells (Pl. 24, figs. 13, 14). Fruits of extant *Cinnamomum camphora* are morphologically and anatomically similar; it is likely, however, that similar fruits could be found among various different extant genera.

Family **LEGUMINOSAE** Juss.

The Leguminosae are represented only by one type of fruit from the Nut Beds locality. Three additional legume fruit types are known from the Clarno Formation (West Branch Creek and Gosner Road localities), and remain to be described. Wood similar to *Acacia* from the Nut Beds (Wheeler and Baas, 1992, fig. 9–13) indicates that arborescent legume taxa were present. The low diversity and relatively low number of specimens of legume fossils in the Clarno Formation suggest that legumes were a relatively minor component of the flora. This is in contrast to the diversity of legume fruits and foliage known from sediments of similar age in southeastern North America (Herendeen and Dilcher, 1990).

Genus **LEGUMINOCARPON** Goeppert

Leguminocarpon sp.

Plate 25, figure 9

Description.—Fruit elliptical, bilaterally symmetrical, laterally flattened in plane of symmetry, about 35 mm long, 12 mm wide, and a few mm thick, base and apex rounded; fruit narrowed over the basal ⅓, possibly where some ovules aborted; fruit body with very fine transverse veins.

Specimen.—OMSI Pb1725.

Discussion.—This specimen is an impression in siltstone from in the leaf layer at the base of Face 3. The texture indicates that it may have been thick-textured, possibly leathery, but not woody. Although it is clearly a pod of the Leguminosae, it does not show the position or orientation of seeds, and on the basis of this single specimen it is not possible to determine the intrafamilial relationships. Lacking additional characters, it is unlikely that the intrafamilial affinities can be determined. Bones (1979, pl. 3, fig. 4) figured another possible legume pod from the Nut Beds (USNM 326716), but the preservation is not good enough to confirm its affinities.

Family **LYTHRACEAE** Jaume St-Hil.

The Lythraceae are a family of about 26 genera of herbs, shrubs and trees with temperate and tropical distribution around the world. The family has an excellent record in the Tertiary of Europe and North America. Both extant and extinct genera have been recognized on the basis of isolated seeds, as reviewed by Tiffney (1981), Friis (1985) and Cevallos-Ferriz and Stockey (1988a). In the Nut Beds this family is represented by fruits and seeds of *Decodon*. In addition, there is some evidence that seeds of *Tripartisemen* (p. 113), which are very common at the Nut Beds, belong to the Lythraceae.

Genus **DECODON** Gmelin

Decodon sp.

Plate 25, figures 1–8

Description.—Fruit a thin-walled, globose, multiseeded capsule, 2.3–3.9, avg. 3.4 mm (SD=0.41, n=5) in diameter, with hypogynous perianth; pedicel at least 3 mm long and 0.4 mm in diameter; fruit multilocular, the number of locules undetermined, with thin septa (0.8–1.2 mm) radiating from a thickened central axis in the basal ⅔ of fruit, placentation axile, seeds numerous; fruit wall thin, 0.8–1.2 mm, approximately equal in thickness to the septa. Seeds anatropous, angular in section, laterally compressed, rounded dorsally, often narrowed and forming a keel ventrally, length 0.7–1.1 mm, width 0.4–0.6 mm; seed coat composed of three layers: 1) innermost layer lining the embryo cavity 18 μm thick, composed of a uniseriate layer of cuboidal cells; 2) middle layer, forming the body of the seed through which the raphe travels, multiseriate, composed of isodiametric cells 10–25 μm in diameter; 3) outer layer uniseriate, composed of thin-walled rectangular cells, this layer 10 μm thick over most of the seed, but dramatically thickened up to 120 μm to form the ventral germination valve, cells of the germination valve anticlinally elongate, 70–120 μm long and 30 μm wide; embryo cavity curved, nearly circular or elliptical in cross section but with a straight ventral margin adjacent to the germination valve; raphe passing through the middle layer of the seed.

Specimens.—UF 6449, pedicellate fruit; UF 5668, 6450, 6451, 9287, fruits with intact seeds.

Discussion.—Several permineralized fruits of *Decodon* have been recovered from the Nut Beds. Sometimes the seed tissues are not preserved and embryo casts are preserved within the empty or carbonaceous mold of the seed (Pl. 25, fig. 1). Serial sections, however, provide excellent details of fruit and seed anatomy (Pl. 25, figs. 2, 4–8). One of the specimens was sectioned longitudinally and clearly shows the pedicel, hypogynous calyx, a thin septum and the thin fruit wall (Pl. 25, fig. 5). These features of the fruit, together with axile placentation and small anatropous seeds with ventral germination valves and curved embryo chambers, indicate affinties with the Lythraceae.

The structure and anatomy of the fossil compare favorably with extant *Decodon verticillatus* (L.) Ell. (cf., Friis, 1985, pl. 15, figs. 10–12; Cevallos-Ferriz and Stockey, 1988a, figs. 19, 20). The Clarno species is distinguished from permineralized remains of *D. allenbyensis* Cevallos-Ferriz and Stockey, from the Eocene of Princeton, southern British Columbia, in the shape of the embryo cavity. In the Clarno fossil, as in *D. verticillatus*, the embryo cavity usually is D-shaped in transverse section because of the relatively straight inner face of the germination valve, but in *D. allenbyensis* the embryo cavity typically is 0-shaped in transverse section, evidently reflecting a convex inner margin of the germination valve.

Decodon has a single extant species, *D. verticillatus*, that is an aquatic shrub of swamps and marshy areas distributed in eastern North America from Ontario to central Florida. The genus was formerly more widely distributed, with many seed records in the Tertiary of Europe (Mai and Walther, 1978; Friis, 1985).

Family **MAGNOLIACEAE** Juss.

The Magnoliaceae are a family of seven genera and about 200 species of trees and shrubs distributed from the Himalayas to Japan and western Malesia, eastern North America to tropical America. The family is divided into two subfamilies (Nooteboom, 1985): the Magnolieae (*Elmerrillia*, *Kmeria*, *Magnolia*, *Manglietia*, *Michelia*, *Pachylarnax*) and the Liriodendreae (*Liriodendron*). Other previously proposed genera of Magnolieae, such as *Talauma* (= *Magnolia*), are dismissed by Nooteboom (1985). The Magnoliaceae are represented in the Nut Beds by at least three species of *Magnolia*. Although wood of *Liriodendron* has been reported from the Clarno "*Osmunda*" locality (Scott and Wheeler, 1982; locality data from Wheeler, pers. comm., 1977), no fruits or seeds of the genus have been recovered from the Nut Beds or any other Clarno localities.

Genus **MAGNOLIA** L.

Leaves of *Magnolia* are reported from several other Tertiary localities in western North America (Taylor, 1990), but, unless confirmed by cuticular characters, the identification of leaves to *Magnolia* should be viewed with caution because *Magnolia* leaves are entire-margined and have a brochidodromous pattern of venation that occurs in many dicotyledonous families.

Two species of *Magnolia* have been identified from the Nut Beds on the basis of woods: *Magnolia longiradiata* and *M. angulata* (Scott and Wheeler, 1982). The xylem of both species appears primitive in relation to that of extant Magnoliaceae in having more bars per scalariform vessel perforation (Scott and Wheeler, 1982).

I recognize three species of *Magnolia* on the basis of seeds from the Nut Beds. There is considerable variation in shape and size among them, however, and it is likely that more species could be recognized using the fine-splitting criteria previously applied for seeds from the London Clay flora (Reid and Chandler, 1933; Chandler, 1961b; see Chandler, 1978, pp. 7–9 for her philosophy of taxonomic splitting as applied to *Magnolia*). The terminology for describing *Magnolia* seeds used below follows that of Tiffney (1977).

Magnolia muldoonae sp. nov.
Plate 26, figures 1–9, 18, 20

Etymology.—This species is named for Maureen Muldoon, recognizing the importance of her assistance with field work at the Nut Beds.

Description.—Infructescence an elongate axis with helically arranged woody follicles; seeds narrowly to broadly ovate, asymmetrical, often dorsiventrally compressed, lensoidal to rounded-triangular in cross section, acutely to obtusely pointed at the micropylar end, rounded basally with a slight bulge at the heteropyle; length 4.0–7.8, avg. 6.0 mm (SD=0.93, n=58), width 2.5–8.4, avg. 4.7 mm (SD=1.44, n=61), thickness 1.5–3.7, avg. 2.4 mm (SD=0.49 n=60); seed cast surface smooth, heteropyle located centrally on the rounded end with a relatively small, circular moat; stalk bowed ventrally at right angles to the long axis of seed; sclerotesta 250 μm thick.

Specimens.—Holotype: UF 6529, infructescence with intact seeds. Paratypes: UF 6546, 6555, 6556, 9728 (22 specimens), USNM 312756 (Bones, 1979, pl. 5, fig. 5), 355378 (6 specimens), 355407 (3 specimens), 355413 (2 specimens), 355421, 355537 (12 specimens), 355540 (20 specimens), 355646 (several specimens), 424697–424699, seed casts.

Discussion.—*Magnolia muldoonae* is the most common species of *Magnolia* in the Nut Beds assemblage, and is particularly abundant in a stratum exposed in the gully between Faces 3 and 4. It is represented by a permineralized infructescence (Pl. 26, figs. 1, 2) and numerous chalcedony seed casts (e.g., Pl. 26, figs. 3–9). The seed casts are usually internal molds of the sclerotesta, and thus present slightly different surface features from the lignitized fossils commonly described in the literature (Mai, 1975; Tiffney, 1977). Although the seeds vary from longer than wide (Pl. 26, figs. 3–5) to wider than long (Pl. 26, figs. 6–8), similarities of the heteropylar region, including the slightly swollen chalaza and ventrally directed stalk (Pl. 26, figs. 7, 8), suggest that they all represent the same species. This is also suggested by the occurrence of numerous seeds of variable length/width ratio together in concentrated pockets in the sediment.

Tiffney (1977) presented a helpful conspectus of extant and fossil magnoliaceous seeds. Seeds with a smooth-surfaced sclerotesta characterize most extant species of *Magnolia*. Seeds of other species of *Magnolia*, including those formerly placed in *Talauma*, and seeds of *Michelia* and *Manglietia*, have verrucate and/or rugulate surfaces. This surface ornamentation carries through to the inside of the sclerotesta, and therefore the smooth surface of the *M. muldoonae* seed casts supports the assignment to *Magnolia*.

The thickness of the sclerotesta as seen in thin-sections of the infructescence is up to 250 μm, as is typical for most extant species of *Magnolia*. Nevertheless, the sclerotesta is thin in relation to that of some other fossil species, such as *M. waltonii* Tiffney (1977) from the Oligocene Brandon Lignite of Vermont and *M. lignita* from the Miocene and Pliocene of Europe (Mai, 1975), which may be 400 to 1000 μm thick. Tiffney (1977, p. 319) reported a single seed from the Clarno Nut Beds locality (HU 59970) that is similar to *M. waltonii* in size, testal wall thickness and chalazal configuration, but noted that further comparison is limited by poor preservation of the Clarno specimen. The specimen may represent an additional species of *Magnolia* that is not considered in this monograph due to insufficient material.

Magnolia paroblonga sp. nov.
Plate 26, figures 10–17

Etymology.—*Para* (Gr = beside, near) + *oblonga*, denoting the similarity of this species to *M. oblonga* Chandler from the London Clay flora.

Description.—Seed cast narrowly to widely subcordiform, asymmetrical, dorsiventrally compressed, more or less lenticular in cross section; length 5.0–7.3, avg. 6.3 mm (SD=0.63, n=17), width 5.5–11.3, avg. 8.5 mm (SD=2.0, n=17), thickness 2.0–4.3, avg. 3.3 mm (SD=0.71, n=17); base truncate, with an elongate chalazal groove that is nearly as long as the seed width, with (in two specimens, UF 9190, 9192) a small central elliptical stalk scar; apex with acute to obtuse micropylar point; lateral margins straight to rounded, sometimes with one or two flat faces (suggesting more than one seed per carpel), often with a faint median ventral groove; inner surface of sclerotesta smooth or with longitudinal striations the chalazal scar.

Specimens.—Holotype: UF 9192. Paratypes: UF 9184–9191, 9192–9196, 9250, USNM 434998–435000.

Discussion.—*Magnolia paroblonga* is represented in the Nut Beds assemblage by internal molds of the seed coat collected at the top of Face 3. The thickness of the sclerotesta is not known. It is readily distinguished from the other Clarno magnolias by longitudinal striations in some of the specimens (Pl. 26, figs. 14–16) and by the elongate chalazal moat (Pl. 26, figs. 14, 15, 17). This elongate groove is a feature shared with *M. longissima* (Bowerbank) Reid et Chandler (1933) and *M. oblonga* Chandler (1961b) of the London Clay flora. Many of the Nut Beds specimens conform with Chandler's diagnosis of *M. oblonga*, but there are also several specimens that are narrower and thicker than those described by Chandler.

Seeds with an elongate chalazal moat are very unusual among extant *Magnolia* species. In reviewing more than 30 species represented in the extant *Magnolia* seed collection prepared by Bruce Tiffney at the Harvard Herbaria, I observed only a single species with this character, *Magnolia quinquepeta* (Bućhoz) Dandy (Arnold Herbarium: Ren Chang Ching 2037) from Chekiang, China. The structure is not obvious on the surface of the sclerotesta, but is seen on the inside surface as a fusiform thickening at the heteropylar end of the endosperm cavity.

Magnolia tiffneyi sp. nov.
Plate 25, figures 10–12;
Plate 26, figure 19

Etymology.—This species is named in recognition of the contributions of Bruce H. Tiffney to the study of fossil *Magnolia* seeds.

Description.—Seed narrowly to broadly ovate, asymmetrical, often dorsiventrally compressed, lensoidal to rounded-triangular in cross section, sometimes with a median longitudinal trough on the ventral side, acutely to obtusely pointed at the micropylar end, rounded at the heteropylar end; length 8.4–12.1, avg. 10.3 mm (SD=1.15, n=10), width 6.0–10.2, avg. 8.3 mm (SD=1.44, n=10), thickness 2.6–4.5, avg. 3.5 mm (SD=0.71, n=8), surface smooth; heteropyle located centrally on the rounded end, not swollen, with a prominent v-shaped moat with stalk oriented more or less parallel to the long axis of seed.

Specimens.—Holotype: UF 6549, seed cast. Paratypes: UCMP 10744, UF 9729–9732, USNM 435002, 435003, UWBM 36070, seed casts; UF 9733, infructescence.

Discussion.—Although *M. muldoonae* is relatively common in the Nut Beds, *M. tiffneyi* is represented only by a few specimens. Seeds of *Magnolia tiffneyi* differ from those of *M. muldoonae* by their large size, the v-shaped rather than rounded moat, and by the lack of a chalazal swelling. In addition, the stalk is oriented more or less parallel to the long axis of the seed rather than bending ventrally (Pl. 25, figs. 11, 12). Seeds of *M. tiffneyi* are similar in size and morphology to those of extant *M. grandiflora* L. of the eastern United States, and to fossils of *M. septentrionalis* Tiffney from the Brandon Lignite of Vermont (Tiffney, 1977).

Family **MENISPERMACEAE** Juss.

The Menispermaceae, or moonseed family, includes about 78 living genera and 520 species. The family consists mostly of woody climbers and, with the exception of a few temperate species, is chiefly tropical, with representatives in Asia, Africa, Australia and America. Menisperms are common "where the canopy is interrupted, e.g. along river banks, margins of forest or in clearings" (Forman, 1986). The Menispermaceae are diverse in the Eocene of Europe as indicated by 15 genera and 22 species recognized in the London Clay (Chandler, 1964). Based upon leaves Wolfe (1977) recognized 11 genera of Menispermaceae from the Paleogene of Alaska.

Fruits of the family are drupes with distinctive endocarps that provide characters important in distinguishing tribes and genera (Diels, 1910; Thanikaimoni, 1984; Forman, 1986). The endocarps are commonly boat-shaped or horseshoe-shaped with various patterns of ornamentation or sculpture and often have a prominent bilobed ventral infold or condyle.

The Menispermaceae are the most diverse family in the Nut Beds with three tribes and 13 genera of fruits: Coscineae (*Anamirta*), Tinosporeae (*Chandlera, Odontocaryoideae, Calycocarpum, Tinospora, Tinomiscoidea, Atriaecarpum, Curvitinospora*) and Menispermeae (*Davisicarpum, Diploclisia, Eohypserpa, Paleosinomenium, Thanikaimonia*). Scott (1954, 1956) described two of the extinct genera, *Chandlera*, and *Odontocaryoidea*, and noted their importance in understanding evolution of endocarp sculpture in the Tinosporeae. In addition, at least four types of menispermaceous leaves are present (Manchester, 1981 and unpublished).

Tribe **COCSINIEAE**

Genus **ANAMIRTA** Colebr.

Anamirta leiocarpa sp. nov.

Plate 27, figures 1–7; Text-figure 14A

Etymology.—*Leio* (Gr = bald) + *karpos* (Gr = fruit), emphasizing the smooth surface of the endocarp.

Description.—Fruit unilocular with a single seed; endocarp globose, diameter 6.2–8.6, avg. 7.5 mm, (SD=0.6 mm, n=5), smooth except for a fine median keel, and the closely adjacent pedicel and style scars; locule subspherical, deeply intruded by a bilobed bulbous condyle; condyle about ¾ as high and ⅓ to ½ as wide as the endocarp and hollow from the base with a median septum, wall of the condyle 0.2–0.3 mm thick; endocarp wall 0.32–0.40 mm thick, composed of fibers 5.0–8.5 μm in diameter, 250 μm long that are oriented periclinally in the ¼ adjacent to the locule, but anticlinally oriented in the outer ¾ of the wall.

Specimens.—Holotype: UF 8745. Paratypes: UF 5712, 6305–6309, 6468, 8728, 8746, USNM 355622, 424641, UCMP 10612, 10613.

Discussion.—*Anamirta leiocarpa* is represented in the Nut Beds by silicified endocarps. Because the outer surface of these endocarps is smooth and rather nondescript (Pl. 27, fig. 1), the species is most easily recognized in broken or sectioned specimens showing the prominent, central, bilobed condyle (Pl. 27, figs. 2–5). Thin sections reveal that the endocarp wall is composed predominantly of anticlinally oriented fibers (Pl. 27, fig. 7). The identification of these fossils as *Anamirta* is supported by the globose form and relatively thin wall of the endocarp, the deeply intruded condyle and by the wall anatomy. *Anamirta leiocarpa* resembles the only modern species of the genus, *A. cocculus* (L.) Wight et Arn. (Pl. 27, figs. 8, 9), in size and endocarp morphology, but *A. cocculus* has a minutely verrucate surface unlike the smooth surface of the fossil.

Extant *Anamirta* is distributed from India to Indochina and throughout Malesia. *A. cocculus* is an inhabitant of lowland areas that occurs, according to Forman (1986) "in a variety of conditions, on banks of rivers and streams, coastal forest, savanahs, on basalt, limestone and sandy soil, both in rain-forest conditions and in seasonal climates. . . , but with a distinct preference for seasonal conditions." Although this is the first confirmation of *Anamirta* based on the fossil fruit record, the genus has also been identified on the basis of fossil leaves from the Eocene Kulthieth Formation of southeastern Alaska (Wolfe, 1977).

Tribe **TINOSPOREAE**

Genus **CHANDLERA** Scott

Chandlera lacunosa Scott

Plate 27, figures 10–20; Text-figure 13B

Chandlera lacunosa Scott 1954, pp. 76–78, pl. 15, figs. 32–41, Scott, 1956, pp. 75–77, fig. 1a.

Description.—Fruit unilocular with a single seed; endocarp oblong, bilaterally symmetrical, rounded-rectangular in dorsiventral view, long-elliptical in lateral view, elliptical in cross section, rounded apically and basally; length 26.5–51.7, avg. 32.7 mm, (SD=4.75, n=22), width 14.7–28.9, avg. 24.3 mm (SD=4.5, n=27), thickness 9.8–23.5, avg. 15.9 mm (SD=3.1, n=27); surface smooth, with a median thread-like longitudinal groove both dorsally and ventrally in the plane of symmetry; endocarp base and apex each with a pair of elliptical apertures (3–4 × 5–7 mm in diameter, located on either side of the plane of symmetry) opening into a system of lacunae; endocarp wall 5–6 mm thick, enclosing eight longitudinal, parallel lacunae, two ventral (condylar) and six lateral; lacunae rounded in transverse section, not connected across the plane of dehiscence, their walls rugulose; the three parallel lacunae in each valve irregularly connected laterally; the lacunae united at their ends and extended outward. Locule cast elongate, straight, boat shaped, length 21.0–39.3, avg. 32.7 mm (SD=4.75, n=22), width 11.5–18.4, avg. 14.7 mm (SD=1.8, n=22); thickness 6.9–13.7, avg. 10.0 mm (SD=1.9, n=22); acute to apiculate at the apex, somewhat less acute at the base, dorsal surface convex, slightly and irregularly sculptured, with a median longitudinal keel; angular in transverse section, each straight segment of the aggregately convex profile opposite a lacuna in the endocarp wall; ventral surface shallowly concave with a median longitudinal keel; placental scar median, subapical on the ventral side.

Specimens.—Syntypes of Scott (1954): UM 29920–29922. Hypotypes: OMSI Pb258, UCMP 10638, UF 9249, USNM 354526, 354532, 354472, 354579, complete endocarps; UCMP 10639, 10640, UF 6844–6847, 6850, 9254, USNM 354474–354476, 354499, 354500, 354510, 354522, 354547, 354548, 354577–354581, locule casts; OMSI Pb243, 171, 253, USNM 354468, 354470, 354473, 354482, 354515, 354516, 354525, 354537, 424848, locule casts surrounded by lacunae casts.

Discussion.—*Chandlera lacunosa* is the largest of the Clarno menispermaceous fruits. It is present throughout the Nut Beds deposit, represented by molds and occasional casts of the endocarp (Pl. 27, figs. 10, 15), and by chalcedony and/or sediment casts of the lacunae (Pl. 27, figs. 12–14) and locule (Pl. 27, figs. 17–20). Fractured specimens show the position of lacunae in the endocarp wall (Pl. 27, figs. 11, 16). I have not observed *Chandlera* at other Clarno localities or elsewhere in the fossil record.

The boat-shaped locule casts with subapical placentation (Pl. 27, fig. 17) and straight longitudinal axis indicate affinity with the menispermaceous tribe Tinosporeae. The endocarp is larger than that of any known living species of the tribe and the endocarp wall is thick relative to that of extant genera of the tribe. Scott (1954, 1956) named and recognized *Chandlera* as an extinct genus in the Tinosporeae. He noted that *Chandlera* is closest to the modern genus *Parabaena* in seed and condyle morphology, but noted that neither *Parabaena* nor any other living genus of Tinosporeae has endocarps with lacunae enclosed in their walls. Scott (1956) pointed out that the rows of spines in endocarps of extant taxa such as *Parabaena* are probably homologous with the intralacunar partitions of *Chandlera*, and suggested that spiny endocarps evolved from unsculptured lacunate endocarps through loss of the outer wall.

Little is known of the dispersal biology of Tinosporeae. Perhaps the spiny endocarps of related modern genera are suitable for animal dispersal, the spines becoming entangled with animal fur, whereas the smooth, lacunose endocarps of *Chandlera* may have been adapted for water dispersal. The system of lacunae within the endocarp wall is a striking feature of this genus, and could have provided buoyancy for water dispersal of the fruits.

Genus **ODONTOCARYOIDEA** Scott

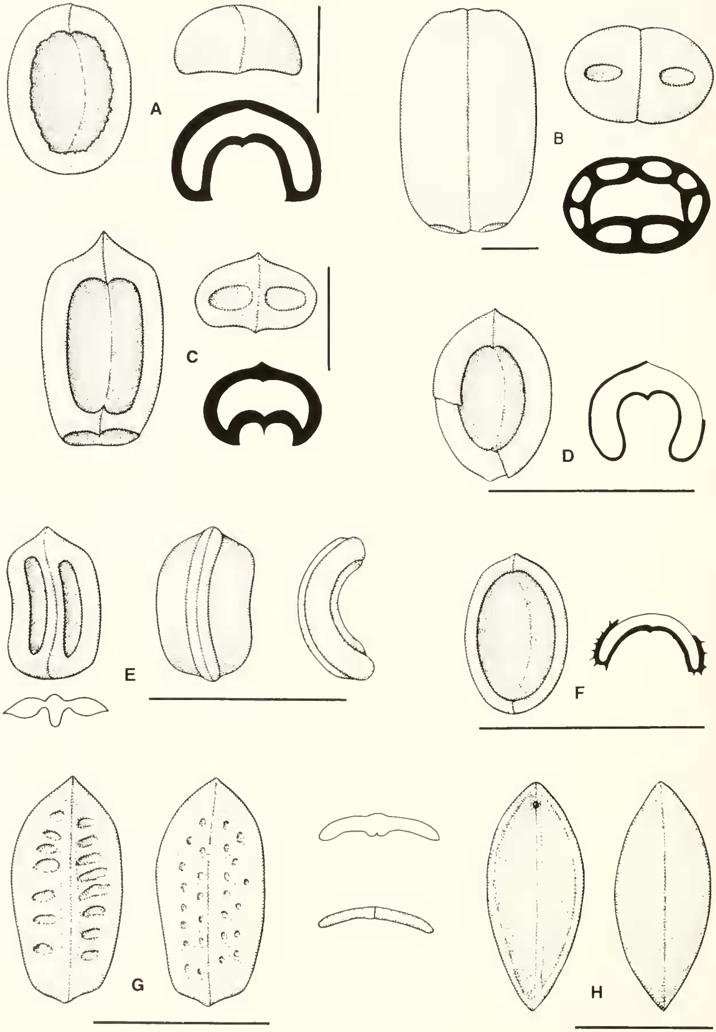
Odontocaryoidea nodulosa Scott

Plate 28, figures 1–10, Text-figure 13C

Odontocaryoidea nodulosa Scott 1954, pp. 74–76, pl. 15, figs. 22–29, Scott 1956, pp. 77–79, fig. 2a–c.

Description.—Fruit unilocular, single-seeded; endocarp oblong, bilaterally symmetrical, pointed apically, truncate basally, crescent-shaped in cross section, length 17.5–28.0, avg. 22.0 mm (SD=3.2, n=11), width 9.0–13.9, avg. 11.0 mm (SD=1.36, n=11), thickness 6.0–10.4, avg. 8.4 mm (SD=1.3, n=11), base with a pair of rounded cavities coalesced across the plane of symmetry, apex with a pair of rounded cavities on either side of the plane of symmetry; dorsal surface convex, finely scabrate to smooth, ventral side hollowed out like a boat, with fine transverse striations; a median longitudinal keel running along the dorsal and ventral surfaces in the plane of symmetry is particularly prominent in the ventral hollow, indicating a bilobed condyle; thickness of lateral limb 3–4 mm; endocarp wall 1.3 mm thick. Locule cast elongate, straight, boat shaped, length 12.9–24.1, avg. 19.8 mm (SD=2.4, n=52), width 8.1–13.0, avg. 10.1 mm (SD=1.1, n=53), thickness 5.6–8.3, avg. 7.0 mm (SD=0.67, n=46), pointed apically, flat basally, dorsal surface convex, smooth, ventral surface concave and transversely ruminate with a grooved median keel over the dorsal and ventral surfaces, placental scar median, subapical on the ventral side.

Specimens.—Syntypes: UM 29915, 29916. Hypo-


A
B
C
D
E
F
G
H

types: UF 6869, 6872, 6874, 6877, USNM 354438, 354453, 354456, 354461, 424850, relatively complete endocarps; HU 60021, 60020, OMSI Pb172 (3 specimens), UCMP 10641–10644, UF 6854–6868, 6870–6876, 6878–6880, UM 29917, 29918, USNM 354441–354455, 354457–354460, 354462–354467, isolated locule casts.

Discussion.—*Odontocaryoidea nodulosa* is the most abundant moonseed in the Nut Beds and occurs throughout the vertical and lateral extent of the deposit. It is represented by locule casts (Pl. 28, figs. 5–9) and occasional casts of the complete endocarp (Pl. 28, figs. 1–4). The locule casts are usually composed of white chalcedony, occasionally of siltstone or sandstone, and sometimes are surrounded by the carbonaceous or permineralized remains of the thick endocarp wall without lacunae (Pl. 28, figs. 5, 10). The locule casts are readily distinguished from those of *Chandlera lacunosa* by the truncate base and smaller size.

This species was described by Scott (1954) as a new genus in the Menispermaceae, tribe Tinosporeae. He noted that genera with endocarps that are straight or only slightly curved from base to apex occur in the tribes Peniantheae, Fibraureae, and Tinosporeae, but observed that "Straight endocarps possessing broad, deep condyles are found only in the Tinosporeae." As its name implies, this genus resembles the modern *Odontocarya* Miers, which occurs from the West Indies and Panama to the Amazon Basin. However, endocarps of the modern genus differ in being smaller, and thinner-walled. *Odontocaryoidea* differ from known living genera by the possession of the paired rounded cavities at the base and apex of the endocarp. Scott (1956) showed how the tridentate apex and base of *Odontocarya* endocarps could be derived by reduction from *Odontocaryoidea*-like structure.

Genus **CALYCOCARPUM** Nutt. ex Torr. et Gray.

Calycocarpum crassicrustae sp. nov.

Plate 28, figures 11–17; Plate 29, figure 1;
Text-figure 13A

Etymology.—*Crassus* (L = thick) + *crusta* (L = shell), referring to the thick wall of the endocarp.

Description.—Fruit unilocular, single-seeded, endocarp subhemispherical, cupshaped, bilaterally symmetrical, elliptical to nearly circular in dorsiventral view, rounded apically and basally, length 19.0 mm, width 13.8 mm, thickness 9.0 mm; surface smooth, except along the ventral rim, which is rugulate; with a longitudinal keel in the plane of symmetry running along the concave ventral and less prominently on the convex dorsal surface of the endocarp; endocarp wall 0.6 (adjacent to the condyle) to 1.2 mm (along dorsal side) thick, without lacunae, composed of fibers 9–20 μm in diameter, more than 250 μm long, mostly periclinal, stratified in layers of varying orientation. Locule cast subhemispherical, cupshaped, bilaterally symmetrical, length 10.8–18.2, avg. 14.6 mm (SD=1.8, n=19), width 8.8–15 avg. 12.5 mm (SD=1.6, n=19), thickness 4.0–10.8, avg. 8.0 mm (SD=1.5, n=19), surface smooth even along the ventral rim, with a median longitudinal keel in the plane of symmetry developed both dorsally and ventrally; placental scar median, subapical on the ventral surface.

Specimens.—Holotype: UF 6769, permineralized endocarp. Paratypes: USNM 424849, complete endocarp cast; UCMP 10564, permineralized endocarp; OMSI Pb173 (2 specimens), 471, 1838, UCMP 10565–10567, 10746, UF 6770–6779, 6781–6787, USNM 354161, 354504, 354505, 424841–424846, 354503 (three incomplete specimens), locule casts.

Discussion.—This species was recovered from siltstone of the lower part of Face 3 as well as from the upper strata of the Nut Beds. It is most commonly preserved as chalcedony locule casts (Pl. 28, figs. 13, 14, 17) that occur loose within the sediment mold of the endocarp. Occasional endocarp casts (Pl. 28, figs. 11, 12) and permineralizations also occur. The holotype is a permineralized endocarp (Pl. 28, figs. 15, 16) that has been sectioned to reveal internal anatomy (Pl. 29, fig. 1).

This fossil species conforms to the Tinosporeae in the large ventral condyle, subapical placenta and median keel. In size and morphology these fruits closely resemble those of extant *Calycocarpum*. Even the rugulate sculpture of the ventral rim of the endocarp (Pl. 28, fig. 12), and contrasting smooth ventral rim of the locule cast (Pl. 28, fig. 14), corresponds to the condition

---

←

Text-figure 13.—Fruits of Menispermaceae, tribe Tinosporeae, from the Nut Beds. **A**, *Calycocarpum crassicrustae* sp. nov., endocarp ventral view, locule cast apical view, endocarp in transverse section. **B**, *Chandlera lacunosa* Scott, endocarp, ventral view (essentially identical to dorsal view), apical view showing pair of apertures, transverse section. **C**, *Odontocaryoidea nodulosa* Scott, endocarp, ventral view, apical view, and in transverse section. **D**, *Tinospora elongata* sp. nov., endocarp, ventral view, with portion of wall removed, revealing smooth surface, and same in transverse section. **E**, *Curvitinospora formanii* sp. nov., locule cast in transverse section, ventral view, dorsal view, and lateral view. **F**, *Tinospora hardmanae* sp. nov., locule cast, ventral view, and in transverse section with portion of spiny endocarp reconstructed based upon incomplete surface molds. **G**, *Atriaecarpum clarnense* sp. nov., locule cast ventral view, dorsal view and in transverse section. **H**, *Tinomiscoidea occidentalis* sp. nov. locule cast apical view, ventral view and dorsal view. Scale bars = 1 cm.

in the extant species. However, the fossil differs from extant *C. lyonii* (Pursh) Gray in having a thicker endocarp wall. The endocarp wall of the extant genus is about ⅓ as thick as that of the fossil (cf. Pl. 28, figs. 16 and 18).

Calycocarpum crassicrustae more closely resembles extant *C. lyonii* than it does "*Calycocarpum*? *jenkensii* Chandler" from the London Clay (Chandler, 1961b). The latter is smaller and shallower than the Clarno and extant species, and probably represents another genus of the Tinosporeae. The only living species, *Calycocarpum lyonii*, is a twining, scrambling, deciduous liana distributed in alluvial woodlands, adjacent wooded slopes and ravines in southeastern North America.

Genus **TINOSPORA** Miers

Tinospora is a genus with about 32 extant species of lianas distributed in tropical Africa, S.E. Asia, Indomalesia, Australia and the Pacific. Referring to the habit of three species common in secondary vegetation in Thailand, in areas where forest has been destroyed or disturbed, Forman (1985) stated that "the exceptional capacity of these climbers to survive damage and to regenerate from detached lengths of stem encourages their spread in these disturbed habitats." The genus is represented by two species in the Nut Beds assemblage.

Tinospora elongata sp. nov.

Plate 29, figures 2–8; Text-figure 13D

Etymology.—*Elongatus* (L = prolonged), referring to the relatively elongate form of the locule cast.

Description.—Locule cast ellipsoidal, bilaterally symmetrical, with a medial dorsal keel in the plane of symmetry and a deep ventral hollow; surface smooth and rounded, slightly pointed apically and less so basally, length 7.7–9.5, avg. 8.4 mm (SD=0.79, n=4), width 4.5–5.8, avg. 5.2 mm (SD=0.60, n=5), thickness 3.8–4.4, avg. 4.1 mm (SD=0.31, n=3); condyle bulbous, 4.8–5.2 mm long, 2.9–4.8 mm wide, intruding about 3.0 mm into the endocarp, with median longitudinal groove; lateral limbs of the locule cast 1.5 mm thick; endocarp wall thin, 0.2 mm in the condyle region.

Specimens.—Holotype: USNM 354502. Paratypes: USNM 355456, 355467, 424648, 424649, 422391, 422392.

Discussion.—*Tinospora elongata* is known from several locule casts. A carbonaceous film between the condyle cast and the locule (Pl. 29, figs. 3, 4) indicates that the endocarp wall was very thin adjacent to the condyle, however the dorsal side of the endocarp remains unknown. The deeply intruded bilobed condyle is best seen in a transversely broken locule cast (Pl. 29, figs. 6–8).

Tinospora elongata closely resembles *T. excavata* Reid et Chandler and *T. wilkinsonii* Chandler of the London Clay flora (Reid and Chandler, 1933; Chandler 1961b) in size and morphology of the condyle and locule cast. However, the Clarno locule casts are somewhat more elongate in outline. It is not known if the endocarps of *T. elongata* were tuburcled on the dorsal surface like those *T. excavata* or perhaps spined as in *T. wilkinsonii*. Among extant species, the endocarps range from smooth-walled to verrucate to spinose (Forman, 1986).

Tinospora hardmanae sp. nov.

Plate 29, figures 9–13; Text-figure 13F

Menispermaceae, Bones, 1979, pl. 1, fig. 10.

Etymology.—Named after Carol Hardman acknowledging her help with field work at the Nut Beds locality.

Description.—Endocarp ellipsoidal, bilaterally symmetrical, estimated dimensions: length 6.8–7.5 mm, width 4.2–4.8 mm, thickness 2.5–3.0 mm; concave ventrally with a deeply intruded smooth-walled condyle, dorsal side convex with closely spaced elongate spines; endocarp wall 0.6–0.8 mm thick; longitudinal keel in the plane of symmetry on the ventral and dorsal surfaces. Locule cast boat-shaped, bilaterally symmetrical, elliptical in dorsiventral view, with a median dorsal and ventral keel in the plane of symmetry, concave ventrally, convex dorsally, rounded apically and basally, but with a slight apical projection from the keel, length 5.6–6.3, width 3.5–4.3, thickness 1.0–1.2 mm, surface smooth; lateral limbs of locule cast 0.8 mm thick, placental scar median, subapical on the ventral side.

Specimens.—Holotype: UF 9255. Paratypes: UF 9256, 9857, 9858, USNM 326715 (Bones, 1979, pl. 1, fig. 10), 354492, 424847.

Discussion.—Among Clarno Tinosporeae, this species has the smallest fruits. *Tinospora hardmanae* is known from locule casts (Pl. 29, figs. 9, 10, 13) and fragments of endocarp molds. Although the endocarp itself is not preserved in these specimens, the narrow space between locule cast and the endocarp mold (Pl. 29, figs. 9, 10) indicates that the endocarp was 0.6–0.8 mm thick. Slender protrusions into the matrix at the basal end of the endocarp mold (Pl. 29, figs. 11, 12) indicate the presence of spines. The locule casts of this species are smaller, thinner, more elongate and more delicate than those described above as *T. elongata*. Also, there is no evidence for spines in *T. elongata*.

Genus **TINOMISCOIDEA** Reid et Chandler

Tinomiscoidea occidentalis sp. nov.
Plate 30, figures 1–5; Text-figure 13H

Etymology.—*Occidens* (L = of the west), denoting the occurrence of this species in western North America.

Description.—Locule cast shaped like a shallow boat, fusiform in dorsiventral view, bilaterally symmetrical, with a median dorsal and ventral keel in the plane of symmetry, base and apex sharply pointed, length 12.0, 16.5 mm, width 5.0, 7.1 mm, thickness 2.5, 3.4 mm; longitudinal axis straight, surface smooth; dorsal face convex, ventral face shallowly concave, with a placental scar subapical along the keel, 2.4 mm below the apex, lateral limbs of locule cast thin (ca. 1.2 mm).

Specimens.—Holotype: USNM 422382. Paratype OMSI Pb926.

Discussion.—*Tinomiscoidea occidentalis* is known only from two locule casts. The specimens closely resemble locule casts of *Tinomiscoidea scaphiformis* Reid et Chandler (1933) from the lower Eocene London Clay flora in size, sharply pointed base and apex and shallow ventral condyle which gives a flattened appearance to the locule cast. The length/width proportions are also similar as indicated by the ratio of 2.3 in the Nut Beds specimens, compared with 1.5–2.2 in the London Clay species.

Reid and Chandler (1933) erected the fossil genus *Tinomiscoidea* to accommodate fossil endocarps and locule casts similar to extant *Tinomiscium* but differing by having the "ventral cavity sharply delimited by faceting of the endocarp wall". The Clarno locule casts show rounded rather than faceted ventral surfaces (Pl. 30, figs. 1–5), and thus differ from the generic diagnosis that was based on *T. scaphiformis*. However, taking into consideration all of the other shared characters, it seems reasonable to place both of these species in the same genus.

Genus **ATRIAECARPUM** Chandler

Atriaecarpum clarnense sp. nov.
Plate 30, figures 6–10; Text-figure 13G

Etymology.—This species is named for the town of Clarno, Oregon.

Description.—Locule cast obovate in face view, bilaterally symmetrical, slightly curved longitudinally; length 9.8–12.8 mm, width 6.6–6.7 mm, thickness 2.0 mm, apex rounded but with a short, beaked tip, base rounded, obtuse, dorsal surface with 4–6 longitudinal rows of about 8 to 12 closely spaced shallow, circular pits; ventral side very slightly concave with a median longitudinal ridge, with a row of at least 10 pits on either side; depressions on ventral side deeper than those on dorsal; thickness of limb 1.7 mm. Endocarp wall 0.3–0.4 μm thick on ventral side.

Specimens.—Holotype: UF 9257. Paratypes: OMSI Pb481, UF 9761, 9762.

Discussion.—Although known only from a few specimens, *Atriaecarpum clarnense* is readily distinguished from other Clarno menisperms by the dimpled dorsal and ventral surfaces. Four of the specimens, including the holotype, are chalcedony locule casts. The other (UF 9761) is a portion of the endocarp preserved in sedimentary matrix, broken and exposing the inside of the ventral endocarp surface. In size and shallow, boat-like morphology it resembles *Tinomiscoidea*; however, it differs by the dimpled sculpture and the lack, or only faint development, of a median longitudinal keel on the dorsal surface.

Atriaecarpum clarnense resembles the London Clay fossil, *A. venablesii* (Chandler) Chandler (1978), in overall shape and surface pitting of the locule cast (cf. Pl. 30, figs. 6–10 with Chandler 1978, pl. 4, figs. 4, 5). The Nut Beds specimens are larger (6.6–6.7 vs. 4.3–5.5 mm wide), and characters of the endocarp, such as the conspicuous protruberances observed in the London Clay species, are not known for the Clarno specimens. Chandler (1978) considered this extinct genus to belong in the Fibraureae tribe rather than in the Tinosporeae because it lacks the deep ventral condyle typical of the latter. However Forman (1985) stated that the Fibraureae and Tinosporeae tribes may not be distinct because of overlap in floral and endocarp characters and in this treatment I have classified *Atriaecarpum* and *Tinomiscoidea* as representatives of Tinosporeae.

Genus **CURVITINOSPORA** gen. nov.

Etymology.—*Curvus* (L = bent) + *Tinospora*, referring to the shape of the endocarp which resembles that of *Tinospora* except in being curved from base to apex.

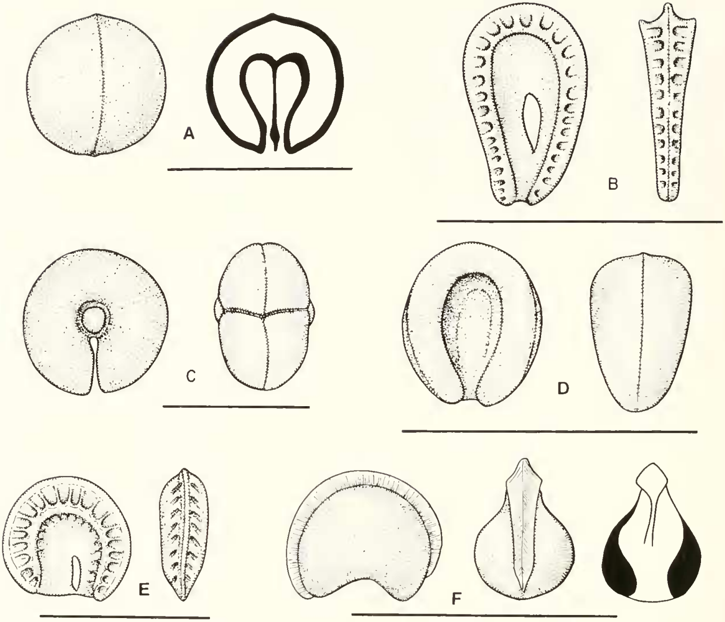
Type species.—*Curvitinospora formanii* sp. nov.

Curvitinospora formanii sp. nov.
Plate 31, figures 1–5; Text-figure 13E

Menispermaceae, Bones, 1979, pl. 1, fig. 9.

Etymology.—Named for L. L. Forman in appreciation of his contributions to the systematics of Menispermaceae.

Description.—Locule cast bilaterally symmetrical, somewhat boat-shaped, but with the long axis uniformly curved from base to apex resulting in a c-shaped lateral profile; base rounded, apex pointed; length 5.1 mm, width 4.6 mm, thickness ca. 2.0 mm; dorsal sur-



Text-figure 14.—Fruits of Menispermaceae, tribes Cocsinieae and Menispermeae from the Nut Beds. **A**, Tribe Cocscinieae: *Anamirta leiocarpa* sp. nov., endocarp in longitudinal view showing dorsal keel, and longitudinal section showing hollow, bilobed condyle about which the locule is curved. **B-F.** Tribe Menispermeae. **B**, *Diploclisia auriformis* (Hollick) comb. nov., endocarp lateral view and front view. **C**, *Eohypserpa scottii* sp. nov., locule cast lateral view, basal view. **D**, *Thanikaimonia geniculata* gen. et sp. nov., locule cast, lateral view, front view. **E**, *Palaeosinomenium venablesii* Chandler, endocarp lateral view, front view. **F**, *Davisicarpum limacioides* sp. nov., endocarp lateral view, front view, longitudinal section. Scale bars = 1 cm.

face convex, with a three-ribbed appearance formed by a prominent median ridge, flanked by a pair of longitudinal grooves, and the broad, rounded longitudinal margins; surface smooth, but with faint broad depressions on the dorsal and lateral faces; ventral surface concave with a median ridge raised more than the lateral edges, thread-like raphe at crest of the median ridge; placentation subapical on the ventral side; with a longitudinal groove on either side of the median ventral ridge.

Specimen.—Holotype: USNM 326714 (Bones, 1979, pl. 1, fig. 9).

Discussion.—Although known only from a single chalcedony locule cast, this species can be placed with confidence in the Menispermaceae by virtue of its boat-shape and subapical ventral placenta. The median keel forms a ridge that is more pronounced both dorsally (Pl. 31, fig. 1) and ventrally (Pl. 31, figs. 2, 3) than in the other Clarno menisperms.

The boat-shaped morphology of the locule in *Curvitinospora* is similar to that of many Tinosporeae. The curvature of the long axis (Pl. 31, figs. 4, 5) brings to mind that of *Hypserpa* (See Forman, 1986, fig. 12 f), and *Eohypserpa*. However, the lateral profile of *Curvitinospora* is C-shaped, whereas that of *Hypserpa*, with both limbs meeting, is O-shaped.

Tribe MENISPERMEAE

The Menispermeae tribe (syn. Cocculeae) is characterized by curved, often horseshoe–shaped, endocarps and seeds. Endocarp sculpture provides good taxonomic features for the tribe (Forman, 1974, 1986). Two genera are present in the Nut Beds assemblage, the fossil genus *Palaeosinomenium* and the living Asian genus *Diploclisia*. Each is represented by a single species, each of which appears to be identical to species from the Eocene London Clay flora. Fruits of this tribe are known from the Paleocene of Germany (Mai, 1989) and North Dakota (Crane et al., 1990).

Genus **DAVISICARPUM** Chandler

Davisicarpum limacioides sp. nov.
Plate 31, figures 10–14; Text-figure 14F

Etymology.—*Limacia* (an extant genus of Menispermeae) + *oides* (Gr = like, resembling), referring to the similarities between this fossil and the extant genus.

Description.—Endocarp subglobose, unilocular bilaterally symmetrical with a curved dorsal horseshoe–shaped ridge forming a keel in plane of symmetry, laterally convex with an inflated condyle; length 4.9 mm, estimated width in plane of symmetry 5.2 mm, thickness across plane of symmetry (and condyle) 3.7 mm; dorsal keel striated perpendicular to its margin but smooth, not fluted; locule horseshoe shaped, situated along the dorsal margin of the fruit, containing a single curved seed; endocarp wall 70–80 μm thick where it surrounds the locule, increased to 550–600 μm thick on the lateral flanks of the condyle; locule lining uniseriate, composed of rectangular cells, 7.5–10 μm high, 7.5–15 μm long, remainder of endocarp formed of periclinally oriented fibers 12.5 μm in diameter in that part of the endocarp forming the wall around the locule, and of isodiametric cells, 10–70 μm in the lateral flanks around the condyle.

Specimen.—Holotype: USNM 435054.

Discussion.—*Davisicarpum limacioides* is known from a single well preserved specimen that was photographed for external morphology (Pl. 31, figs. 10–12) and then sectioned transversely to show internal structure (Pl. 31, figs. 13, 14). In lateral view it resembles endocarps of various genera of the Menispermeae tribe such as *Palaeosinomenium* (Pl. 29, fig. 17), however the keel is not fluted, and in transverse view the lateral margins are seen to be inflated and markedly convex, rather than concave. The condyle was probably more or less hollow originally and subsequently filled with sediment when the fossil was deposited.

This species is similar to *Davisicarpum gibbosum* Chandler from the London Clay (Chandler, 1961b, 1978), but is smaller (width 5.2 vs 7.1–7.5 mm, length 4.9 vs 6.5–7.5 mm). Chandler (1978) noted that *Davisicarpum* shows the closest resemblance to extant *Limacia*. Both genera have a curved locule and an inflated condyle resulting in markedly convex lateral margins. The structure of the *Limacia* endocarp in longitudinal section is shown by Forman (1986, fig. 12r) and is very similar to that of *D. limacioides* (Pl. 31, figs. 13, 14; Text-fig. 14F). Justifying continued retention of the fossil generic name *Davisicarpum*, Chandler (1978) noted a consistent morphological difference between the London Clay species and *Limacia* that also holds true for the Clarno specimen: "In *Limacia oblonga* (Wall) Miers the locular rim is continued further towards the attachment than in *Davisicarpum* so as to leave a small gap only between the ends of the limbs, whereas in *Davisicarpum* the gap is much wider." The endocarps of *L. oblonga* are two to three times larger (15 mm high and wide) than the fossil specimens. The other two extant species, *Limacia scandens* Lour. and *L. blumei* (Boerl.) Diels, have not been examined in relation to the fossil material; fruiting material is not currently available among the collections of *L. blumei* (Forman, 1986). Nevertheless, *Davisicarpum* is clearly a close relative of this living genus.

Limacia has three extant species that are woody climbers in tropical southeastern Asia and Malesia (Forman, 1986). Wolfe (1977) recognized leaves of *Limacia* from the middle Eocene Kushtaka Formation of Alaska.

Genus **DIPLOCLISIA** Miers

Diploclisia auriformis (Hollick) comb. nov.
Plate 30, figures 11–14; Text-figure 14B

Carpolithes auriformis Hollick 1936, p. 170, pl. 120, fig. 7.
Diploclisia bognorensis Chandler 1961b, p. 161, pl. 16, fig. 14–17.
Dipoclisia, Bones, 1979, pl. 2, figs. 2, 3.

Description.—Fruit unilocular, single-seeded, endocarp laterally compressed in plane of bisymmetry, obliquely obovate in lateral view with broad-rounded dorsal surface and acute-rounded base; length 6.3–8.0, avg. 7.0 mm (SD=0.75, n=5), width 4.0–6.8, avg. 4.9 mm (SD=1.20, n=5), thickness 1.4–1.5, avg. 1.47 mm (SD=0.60, n=5); with a keel running along the dorsal surface in the plane of symmetry; both lateral margins bearing a horseshoe-shaped ridge separating dorsal and ventral ornamentation; dorsal side of the ridge marked with 25 to 30 radially aligned ribs alternating with rounded pits or grooves; inner or ventral flank of the ridge smooth and concave, with an obliquely oriented, elliptical foramen. Locule cast conforming in morphology and ornamentation to endocarp, horseshoe-shaped with approximately equal limbs.

Specimens.—UCMP 10558, 10559, UF 6484, 6485, 6486, USNM 312648 (Bones, 1979, pl. 2, fig. 3), 312749 (Bones, 1979, pl. 2, fig. 2), 354508, 354571, 354573, 446069.

Discussion.—This species is represented in the Nut Beds by carbonaceous endocarp compressions (Pl. 30, figs. 12, 13) and chalcedony locule casts (Pl. 30, figs. 11, 14). The compressions closely resemble those of *Carpolithes auriformis* Hollick from a Paleogene locality on the south shore of King Salmon Lake, Alaska Peninsula (Hollick, 1936, pl. 120, fig. 7), and the casts closely resemble those described as *Diploclisia bognorensis* from the London Clay (Chandler, 1961b). These occurrences appear to represent a single morphological species. Endocarps with the horseshoe shaped locule and fluted dorsal surface are diagnostic of the Menispermaceae, tribe Menispermeae.

Diploclisia occurs today in East Asia, China and Burma to India and the Malay Peninsula. In reference to specimens of this species from the London Clay flora Chandler (1961b, p. 162) stated that "The form and structure are so closely comparable with the living *Diploclisia* that there can be no doubt of the relationship." Among the most similar extant species are *D. affinis* Diels and *D. chinensis* Merrill. Endocarps of *D. affinis* (specimen examined E.H. Wilson 2286 from western Hupeh, China) are particularly similar in size, shape, number of ribs, and the smooth ventral surface to the fossil species.

Genus **EOHYPSERPA** Reid et Chandler

Eohypserpa scottii sp. nov.

Plate 29, figures 14–16; Text-figure 14C

Etymology.—This species is named for Richard A. Scott, recognizing the importance of his contributions to fossil Menispermaceae.

Description.—Fruit subglobose, nearly circular in lateral view; locule cast bilaterally symmetrical, smooth, prominently curved with base and apex nearly touching, width across plane of symmetry 7.3 mm, diameter in plane of symmetry 8.5–11.5 mm; median keel in the plane of symmetry on the dorsal (and ventral?) surface becoming more prominent at the apical end, apical limb pointed, basal limb blunt-rounded; with a central circular aperture 2–2.5 mm in diameter on each lateral face, about which the locule is curved.

Specimens.—Holotype: USNM 354506. Paratype: USNM 446075.

Discussion.—*Eohypserpa* is represented by two locule casts from the Nut Beds. Although the endocarp itself is not preserved, the locule morphology is very distinctive and is similar that of extant *Hypserpa* (see Forman, 1986, fig. 12). In both there is a central pair of lateral apertures in the endocarp about which the locule is curved. Locule casts of *Eohypserpa scottii* resemble those of the London clay species, *E. parsonii* Reid et Chandler (1933), in general form, smooth surface and size. The London Clay species was diagnosed largely on the basis of endocarp features that are not preserved in the Nut Beds specimens.

Reid and Chandler (1933) observed the striking similarity between the London Clay endocarps and those of extant *Hypserpa*, but reported several differences that led them to place the fossils in an extinct genus. These differences include the following: 1) Reid and Chandler stated that the fruits of extant *Hypserpa* are more compressed laterally, whereas those of the London Clay are typically more globose [however, there is overlap in this feature]; 2) In *Hypserpa* the curvature of the carpel is less symmetrical than in the London Clay fossils; 3) In *Eohypserpa* the cross section of the locule is more elongate but more sharply curved at the cusps than in the living genus, and the lateral cavities are relatively larger; 4) The fossil endocarps from the London Clay are transversely ribbed, but not tubercled or angular as in *Hypserpa*.

It is not known whether the Clarno species had a transversely striate endocarp as in the London Clay genus, or a verrucate endocarp as in extant species of *Hypserpa*. However, the available characters including symmetry of the locule, curvature and size of the lateral cavities, and smoothness of the locule support placement of the Clarno species in *Eohypserpa* rather than *Hypserpa*.

Genus **PALAEOSINOMENIUM** Chandler

Palaeosinomenium venablesii Chandler

Plate 30, figures 15–20; Text-figure 14E

Palaeosinomenium venablesii Chandler 1961b, pp. 159–160, pl. 16, figs. 9–13.

Description.—Fruit unilocular, single-seeded, endocarp laterally compressed in plane of bisymmetry, obliquely ovate in lateral view, with broad-rounded dorsal margin and straight ventral margin, endocarp length 2.1, 3.5, 3.7 mm, width 2.3, 4.4, 4.3 mm, thickness 1.0, 1.9, 1.9 mm; dorsal margin of endocarp with a prominent median keel in the plane of symmetry (0.4–0.5 mm high); both lateral faces with a broad, shallow concavity rimmed by a C-shaped ridge separating dorsal and ventral ornamentation; each lateral face with 18–21 radially aligned ridges alternating with rounded grooves that are developed both ventrally and dorsally; an obliquely oriented narrow foramen is situated medially near the base. Locule cast obliquely C-shaped with the two arms of unequal length, one of the arms blunt-tipped, the other tapered to a point, not as sharply sculptured as the endocarp, fluted dorsally with 14–17 depressions, smooth ventrally; length 2.0–4.1, avg. 2.9 mm (SD=0.61, n=41), width 2.3–4.3, avg. 3.3 mm (SD=0.56, n=41), thickness 0.81-2.60, avg. 1.33 mm (SD=0.37, n=41), ventral margin markedly concave, dorsal margin convex.

Specimens.—USNM 354461, 424815, 424826, endocarp casts; HU 60018, 60019, UCMP 10560–10563, UF 6487–6491, 6737, USNM 354494 (17 specimens), 354489 (6 specimens), 354491 (5 specimens), 354493, 354514, 354559–355567, 424812–424814, 424816–424840, 435101, locule casts.

Discussion.—This species is known from the Nut Beds mostly from isolated chalcedony locule casts (Pl. 30, figs. 19, 20). Molds in the matrix from which the locule casts were removed show the impression of the endocarp surface (Pl. 30, fig. 15). Rarely, specimens are preserved as endocarp casts showing the exterior sculpture (Pl. 30, figs. 16–18). In all observable characters, the Clarno specimens are indistinguishable from the London Clay specimens named *Palaeosinomenium venablesii* Chandler, although details of internal anatomy described by Chandler (1961b) are not preserved in the Clarno specimens.

Palaeosinomenium endocarps and locule casts bear some resemblance to those of *Diploclisia* described above, reflecting their common affinities within the tribe Menispermeae. However, *P. venablesii* is readily distinguished from *D. auriformis* by a smaller length/width ratio, by the unequal length of the limbs, and by the presence of ventral sculpture. Similar extant genera in the Menispermeae include *Menispermum* and *Sinomenium*. But according to Chandler (1961b), they are distinguished from the fossil by being less oblique and having shorter, rounder foramina. *Cocculus* endocarps are more rounded and inflated than those of the fossil, and *Cissampelos* has a median groove instead of a median keel.

Genus **THANIKAIMONIA** gen. nov.

Etymology.—This genus is named in memory of G. Thanikaimoni, recognizing his contributions to the morphology and systematics of Menispermaceae.

Type species.—*Thanikaimonia geniculata* sp. nov.

Thanikaimonia geniculata sp. nov.
Plate 31, figures 6–9; Text-figure 14D

Etymology.—*Geniculate* (L = like the bent knee), referring to the strongly curved locule cast.

Description.—Locule cast obovate, horseshoe-shaped, bilaterally symmetrical, length 5.3 mm, width in plane of symmetry 4.3 mm, thickness across plane of symmetry 4.0 mm, dorsal and ventral surfaces smooth, with a median dorsal keel in the plane of symmetry; both lateral faces with a prominent median concavity about which the seed cavity is curved; limbs of the seed cavity nearly equal in length, but with one broader and more rounded at its extremity than the other, the broader one with a circular scar at its tip.

Specimen.—Holotype: USNM 355480.

Discussion.—This species is represented by a single locule cast showing a horseshoe-shaped seed cavity (Pl. 31, figs. 7, 8) with a median dorsal keel in the plane of bisymmetry (Pl. 31, figs. 6, 9). In general form the locule cast of *Thanikaimonia* resembles that of *Diploclisia*, but it differs by the lack of surface sculpture and by its greater thickness across the plane of symmetry. Smooth locules occur among extant Menispermeae, as in *Pachygone*, but no close morphological match to this fossil has been found among extant genera.

Family **MUSACEAE** Juss.

The Musaceae (banana family) have three modern genera of old world tropical distribution: *Musa* L. (35 spp.), which is restricted to Asia, *Ensete* Horan. (7 spp.) of Asia and Africa, and *Musella* C.Y. Wu ex H.W. Li (1 sp.), in southern China. *Ensete* was treated as a subgenus of *Musa* prior to its recognition as a genus by Cheesman (1947), and *Musella* was only recently segregated from *Ensete* (Wu, 1981). Features distinguishing *Ensete* from *Musa* include persistent bracts and flowers, warty rather than granular pollen, and larger seeds with a deeply recessed hilar cavity. *Musella* differs from the other two genera by its short stems and congested rhizomatous growth.

Genus **ENSETE** L.

Ensete oregonense Manchester et Kress
Plate 32, figures 1–14, 16–19

Ensete oregonense Manchester et Kress 1993, pp. 1264–1272, figs. 2–11, 37.

Olacaceae, Bones, 1979, pl. 5, fig. 1.

Description.—Seed anatropous, subfusiform-ellipsoidal when complete, circular to subangular in transverse section, base rounded, apex truncate; length of complete seed 10.0–12.0, avg. 10.8 mm (SD=0.96, n=4), width 5.3–7.2, avg. 5.8 mm (SD=0.43, n=15), with a wide hilar depression, and an operculum (micropylar plug) about 1.2 mm in diameter; hilar rim ca. 1 mm high; outer surface of seed smooth to finely striate longitudinally; seed coat of two layers, each 200–250 μm thick and composed of longitudinal fibers, the inner layer diverging from the outer seed coat near the base and apex of the seed, delimiting a chalazal mass at one end, a micropylar collar at the other, and a central barrel-shaped embryo/endosperm chamber; embryo small, 2.5 mm long, straight and bulbous, ascending from the channel delimited by the micropylar collar into the central chamber. Length of specimens with hilar rim broken away 6.1–10.0, avg. 7.5 mm (SD=0.98, n=15); Length of central chamber (from casts missing both the chalazal mass and hilar rim) 4.3–8.5, avg. 6.0 mm (SD=0.84, n=47), width 5.3–7.2, avg. 5.8 mm (SD=0.43, n=15).

Specimens.—Holotype: UF 6621. Paratypes: HU 59915, 60039, 60041, OMSI Pb1061, 1314, 1842, UCMP 10688–10695, UF 6611–6620, 6622–6642, 6726, 9739, USNM 326732 (Bones, 1979, pl. 5, fig. 1), 354608–354613, 354615–354617, 354621–354625, 354626, 424620, 434966–434982, UWBM 35274, 36056, 36080.

Discussion.—Seeds of *Ensete* are especially common in the Nut Beds. They occur in the basal leaf layer in Face 4, and are common at the top of Face 3. The seeds are preserved in different fashions. Most are chalcedony infillings of the central chamber of the seed. These are barrel-shaped casts with a depression and circular mark at both ends, sometimes with adhering remnants of tegmen and testa (Pl. 32, figs. 3–5, 8, 9). Occasional specimens are more complete, with the chalazal region intact showing the rounded base. In these the profile of the seed is faintly constricted in the position corresponding to the septum separating the central chamber and chalazal mass (Pl. 32 figs. 6, 10). The seeds usually are preserved with the operculum detached, exposing the micropylar collar. Longitudinal sections reveal that the seeds are bitegmic (Pl. 32, fig. 14), with the tegmen diverging from the testa near the base and apex of the seed, delimiting the chalazal mass at one end and the micropylar collar at the other, and a central barrel-shaped endosperm/embryo chamber. A small straight embryo protrudes into the endosperm chamber from the micropylar end (Pl. 32, figs. 12, 13). A few specimens show a conical projection at the micropylar end (Pl. 32, fig. 4) corresponding in position to the "nucellar pad" of McGahan (1961). In a few cases the operculum is preserved (Pl. 32, fig. 16).

The affinities of these and other fossil and extant seeds of Zingiberales were treated in detail by Manchester and Kress (1993). *Ensete oregonense* seeds conform to those of the Musaceae in the thick seed coat, well-defined micropylar collar, operculum, and a septum dividing the embryo chamber from the chalazal mass. *Ensete* is differentiated from *Musa* by its tendency for larger seeds (1 to 2.5 cm), and an enlarged hilar depression. The fossil seeds are at the high end of the size range for extant *Musa* seeds and at the low end of the size range for extant *Ensete* seeds. The fossils clearly belong to *Ensete* because of the enlarged hilar depression (cf. pl. 32, fig. 15).

This species is the only known record of Musaceae based upon seeds from North America. Although no musaceous leaves have been confirmed from the Nut Beds, it is likely that there are significant taphonomic biases against transport of large, persistent leaves to sites of deposition, whereas the seeds could easily have been carried by birds and/or water runoff. The confirmation of *Ensete* seeds in the North American Tertiary lends credence to the identification of the family based on leaves of *Musophyllum complicatum* Lesquereux from the Eocene Green River Formation of Wyoming (Lesquereux, 1878, pl. 15, fig. 1–6).

Family **PALMAE** Juss.

The Palmae (palm family) are represented in the Nut Beds by silicified stems and petioles and by *Sabal*-like leaf impressions (Manchester, 1981) as well as by seeds. Two species of *Sabal* are recognizable on the basis of seeds. Previous reports of palm seeds from the Nut Beds (e.g., Bones, 1979) were based upon specimens that I have dismissed from the Palmae and treated here as *Coryloides* in the Betulaceae.

Genus **SABAL** Adans.

Sabal is a genus of 15 extant species distributed in the southeastern United States and Mexico, the West Indies and northern South America (Zona, 1990). The genus has also been confirmed on the basis of cuticularly preserved costapalmate leaves from the Eocene of Tennessee (Daghlian, 1978), and from seed remains from the Tertiary of Europe (Mai, 1976). The two species of *Sabal* seeds from the Nut Beds are considered below.

Sabal bracknellense (Chandler) Mai
Plate 33, figures 1–3

Palmospermum bracknellense Chandler 1961b, pp. 125–126, pl. 13, figs. 15, 16.
Sabal bracknellense (Chandler) Mai 1976, pp. 104–105, pl. 2, figs 5–9.
Palmae, Bones, 1979, pl. 1, fig. 3.

Description.—Seed cast globose to oblate, circular in dorsiventral plane section, rounded dorsally, truncate ventrally, height and width 3.8–5.3, avg. 4.3 mm (SD=0.48, n=14), dorsiventral thickness 4.0–6.8, avg. 4.7 mm (SD=0.66, n=15); ventral truncation circular, shallowly depressed, with a central circular raised area 1.2–2.0 mm in diameter; sometimes with a shallow longitudinal groove passing over the rim of the ventral truncation; rim around the truncation rounded, faintly ruminate; otherwise, seed surface smooth, occasionally with a small circular dome-like area on the surface representing protrusion of the embryo.

Specimens.—UF 8484–8491, USNM 354662 (7 specimens), UCMP 10720–10727.

Discussion.—This is the more common species of

Sabal in the Nut Beds assemblage. Although preserved only as internal molds of the seed coat, without details of anatomy, these specimens correspond very closely in size and morphology to seeds of *Sabal bracknellense* (Chandler) Mai from the Eocene London Clay (Chandler, 1961b) and Geiseltal (Mai, 1976) floras. The circular dorsiventral outline, and ventral depression with central hilum (Pl. 33, figs. 1–3) are characters diagnostic of extant *Sabal*. Referring to *Palmospermum jenkinsii*, *P. bracknellense* and *P. cooperi* from the London Clay, Mai (1976, p. 105) questioned why Chandler included these species in a form-genus for palm seeds of unknown affinities: "The characteristics of all these species speak very distinctly for their placement in the genus *Sabal* Adans."

Sabal jenkinsii (Reid et Chandler) comb. nov.

Plate 33, figures 4–8

Palmospermum jenkinsi Reid et Chandler 1933, p. 110, pl. 1, figs. 23, 24.

Description.—Seed cast globose to oblate, circular in dorsiventral view, rounded dorsally, truncate ventrally; height and width 7.3–9.0 mm, dorsiventral thickness 5.7–7.4 mm; ventral truncation circular, shallowly depressed, with a central raised area 2.2 mm in diameter, from which cells radiate; with a shallow longitudinal raphe groove passing over the rim of the ventral truncation; seed surface smooth, with a small circular dome representing the protruding embryo visible on some specimens; seed coat 130 μm thick, of two layers, inner layer darker, 20–30 μm thick composed of uni- or biseriate row of rectangular cells, outer layer lighter, not well preserved appearing almost gelatinous but with sharp boundaries, 100 μm thick; with an additional layer of sclerenchymatous tissue sometimes preserved in the ventral depression.

Specimens.—OMSI Pb1812, UF 9751–9754, USNM 326713 (Bones, 1979, pl. 1, fig. 3).

Discussion.—*Sabal jenkinsii* is represented in the Nut Beds only by a few specimens from the top of Face 3. In one of the specimens a thickened patch of the seed coat is preserved in the ventral hollow (Pl. 33, fig.7). One specimen still partially embedded in the sedimentary matrix was sectioned to show the bilayered wall structure (Pl. 33, fig. 8).

This species corresponds to *Sabal* in overall shape, seed coat thickness, and configuration of the ventral depression. Just as in extant seeds of the genus, the seed coat is thickened in the hilar region much more than it is over the body of the seed. The main difference between this species and *S. bracknellensis* is the larger size. This species conforms to the diagnosis of *Palmospermum jenkinsii* Reid et Chandler (1933), and following the suggestion of Mai (1975), is hereby transferred to *Sabal*.

Family **PLATANACEAE** Dumort.

The Platanaceae are a family of one extant genus and about 7 species of trees. The family has an excellent fossil record that includes inflorescences and infructescences extending into the mid-Cretaceous (Friis, et al., 1988). The Platanaceae are represented in the Nut Beds by wood of *Plataninium* (Scott and Wheeler, 1982), leaves of *Macginitiea* (Manchester, 1986) and the three genera of platanaceous infructescences treated below: *Macginicarpa*, *Platanus*, and the new genus *Tanyoplatanus*.

Macginicarpa glabra Manchester

Plate 33, figures 9–12

Macginicarpa glabra Manchester 1986, p. 209, figs. 20–37, 44.

Description.—Infructescence spheroidal, 9–15 mm in diameter, consisting of a central receptacular core 3–6, avg. 4.5 mm in diameter surrounded by about 60 closely packed florets; florets hypogynous, each containing five, very rarely six, apocarpous achenes arising from a pentagonal (rarely hexagonal) receptacle, surrounded by a perianth of 15–30 tepals; tepals extending as high as the achenes, 3.5 mm long, 0.6–1.0 mm wide, and 0.13–0.5 mm thick, outer tepals thicker than inner, but perianth not differentiated into petals and sepals; achenes free, arranged in a single whorl with ventral sutures contiguous about the floral midline, achene body ovoid to ellipsoidal, less commonly obovoid 3–4 mm long, 0.5–1.2 mm wide, 0.7–1.5 mm deep in predispersal state, 5–8 mm long and 2.5–3.0 mm wide or deep at maturity, with a persistent style up to 2.3 mm long, slightly curved, with a ventral slit running its full length; achenes glabrous, pericarp consisting of: the exocarp, with a thin uniseriate layer of cutinized epidermal cells, the mesocarp, composed mainly of isodiametric parenchyma cells 35–50 μm in diameter, and the endocarp, made up of a uniseriate layer of anticlinally elongate, thick-walled cells, 7–10 μm wide, 60 μm high.

Specimens.—Holotype: UF 5153. Additional specimens: UF 5153–5159, 5161–5164, USNM 354077–354083, 354090–354092, 354095, 354097, 354104–354106, 354115, 354116, 354119–354140, 354142–354148, 354150, 354151, 354587.

Discussion.—*Macginicarpa glabra* infructescences are one of the most abundant reproductive structures in the Nut Beds deposit. They are preserved both as compressions and as permineralizations. Excellent anatomical details are provided by permineralized fruits that have been fractured (Pl. 33, fig. 9) and/or sectioned (Pl. 33, figs. 10–12). The same species occurs at several other localities in the Clarno Formation, consistently associated with digitately palmately lobed leaves of *Macginitiea angustiloba*. Based upon shared platanaceous affinity, and co-occurrence at several localities, I have suggested that the *M. angustiloba* leaves belonged to the same plant that produced *Macginicarpa* infructescences—a plant informally termed the Clarno plane tree (Manchester, 1986). Silicified staminate inflorescences (*Platananthus synandrus* Manchester, Pl. 33, fig. 13), isolated stamen groups (*Macginistemon mikanoides* [MacGinitie] Manchester) and platanaceous wood (Scott and Wheeler, 1982) from the Nut Beds are also hypothesized to correspond to the Clarno plane tree (Manchester, 1986).

Macginicarpa glabra conforms to the Platanaceae in the possession of unisexual globose heads of numerous florets each bearing several achenes with persistent styles and long ventral sutures. However, the species differs from living species of *Platanus* because: 1) it has a relatively well developed perianth, 2) the number of achenes per floret is relatively constant at five, rather than variable within the head, 3) the achenes usually are ovoid rather than obovate, 4) dispersal hairs are lacking. The lack of dispersal hairs in achenes of *Macginicarpa* suggests that these fruits were not as well adapted for wind dispersal as those of extant *Platanus* (Manchester, 1976). Infructescences of *Macginicarpa* are also known from the Early Eocene of Chalk Bluffs, California, Middle Eocene of Republic, Washington (Manchester, 1986), and from the Paleocene of Joffre Bridge, Alberta (Pigg and Stockey, 1991), but are not known from the European or Asian Tertiary.

Genus **PLATANUS** L.

Platanus hirticarpa sp. nov.

Plate 33, figure 14; Plate 34, figures 1–4

Etymology.—*Hirtus* (L = hairy, shaggy) + *karpos* (Gr = fruit), referring to the presence of dispersal hairs on the fruitlets.

Description.—Infructescence spheroidal, 8.0 mm in diameter, consisting of a central receptacular core ca. 2 mm in diameter surrounded by numerous closely packed florets; florets hypogynous, each containing four (or more?), apocarpous achenes, surrounded by a perianth of about 15 tepals; tepals extending as high as the achenes, 2.2 mm long, 0.5–1.0 mm wide, and 20–30 μm thick, outer tepals thicker than inner, but perianth not differentiated into petals and sepals; achene body obovate to obtriangular in longitudinal outline, with a persistent style up to 2.3 mm long, slightly curved, with a ventral slit running its full length; achenes enveloped with numerous hairs that arise from the lower portion of the fruit, these hairs large, 24–29 μm in diameter, 1250–1500 μm long, uniseriate-multicellular, composed of cells 80–100 μm long.

Specimens.—Holotype: UF 5160.

Discussion.—In contrast to *Macginicarpa* which is abundant in the Nut Beds, extant *Platanus* is known only from a single infructescence. At the time *Macginicarpa* was described (Manchester, 1986), I didn't know that *Platanus* was present as well. In addition to the infructescence described above, *Platanus* is now known from rare isolated achenes with the characteristic dispersal hairs as compression fossils from three other Clarno localities (West Branch Creek, White Cliffs, Sheep Rock Creek).

On the basis of infructescence morphology (Pl. 33, fig. 14), achene shape (Pl. 34, figs. 2, 3) and presence of dispersal hairs (Pl. 34, fig. 4), I consider that this fossil belongs to the extant genus. *Macginicarpa* and the Cretaceous platanaceous infructescences known as *Platanocarpus* Friis, Crane et Pedersen (1988) differ from *Platanus* because the achenes lack dispersal hairs. *Macginicarpa* is also distinguished by ovate, rather than obtriangular, achenes. *P. hirticarpa* represents the earliest record of extant *Platanus* to be confirmed by fruit structure, and shows that both extant and extinct genera of Platanaceae coexisted in the early Tertiary. Platanaceous leaves that appear to represent *Platanus*, and not *Macginitiea*, are now known from the White Cliffs Clarno locality, although they have not been recovered from the Nut Beds.

Genus **TANYOPLATANUS** gen. nov.

Etymology.—*Tanyo* (Gr = elongate) + *Platanus* (Gr = plane tree), referring to the elongate infructescences of this platanaceous plant.

Type species.—*Tanyoplatanus cranei* sp. nov.

Tanyoplatanus cranei sp. nov.

Plate 34, figures 5–15

Etymology.—The epithet is named after Peter R. Crane, recognizing his contributions to paleobotany including the fossil record of Platanaceae.

Description.—Infructescence elongate-cylindrical, up to at least 30 mm long, 5.0, 10.0, 11.0 mm in diameter, consisting of a straight central axis 1.6–2.8 mm in diameter surrounded by numerous closely packed florets; florets hypogynous, each containing three to four apocarpous achenes, surrounded by a perianth of about five to ten thin tepals; tepals extending as high as the achenes, perianth not differentiated into petals and sepals; achene body ovate to less commonly obovate in longitudinal outline, up to 1.1 mm in diameter, 3.4 mm long, tapered to a persistent style, with a ventral slit running its full length; numerous hairs arising from the lower portion of the fruit and receptacle; hairs large, 20 μm in diameter, more than 500 μm long, uniseriate-multicellular, the cells 80–100 μm long. Achene anatomy: most of the achenes infertile, lacking locule development, composed of angular parenchyma cells; occasionally achenes fertile, with a single locule and seed; locule lining comprising a uniseriate layer of tall columnar cells, 50–80 μm high, 10–12 μm wide, surrounded by mesocarp of angular parenchyma cells 40–70 μm in diameter, with about three vascular bundles, exocarp uniseriate layer of small rectangular cells about 5 μm thick and 10–12 μm long.

Specimens.—Holotype: USNM 424876. Paratypes: OMSI Pb923, UF 5671.

Discussion.—*Tanyoplatanus* is represented by three permineralized specimens from the Nut Beds, and by a few compression specimens from the West Branch Creek and White Cliffs Clarno localities. The general appearence is that of an elongate bottle brush or test tube brush with numerous florets arranged about an elongate axis. Although general aspects of the morphology are apparent from longitudinally fractured specimens (Pl. 34, figs. 5, 7), it was necessary to prepare serial transverse (Pl. 34, fig. 6) and longitudinal sections (Pl. 34, figs. 7–11, 13–15) and acetate peels of the infructescences to document anatomical details.

The infructescences of all previously described fossil and extant Platanaceae are more or less globose. *Tanyoplatanus* compares favorably with *Platanus* in the morphology and anatomy of achenes and in the arrangement of florets on an expanded receptacular core. It differs by the elongated nature of the infructescence and by the relatively small number of achenes per floret (3–4 vs. 4–9). Although this is the first formal description of the taxon, the genus has been illustrated previously and described as "elongate infructescence" (Crane et al., 1990) from the Paleocene of North Dakota, and I have collected it at several localities of the Paleocene Fort Union Formation in Wyoming. Both in these Paleocene localities and at the Clarno West Branch and White Cliffs localities, compound leaves of *Averrhoites affinis* (Newberry) Hickey co-occur, and it is possible that these *Sapindopsis*-like leaves and infructescences were borne by the same taxon.

Unlike *Macginicarpa*, and like *Platanus*, the fruits of *Tanyoplatanus* bear numerous dispersal hairs (Pl. 34, fig. 14). The perianth is not as well developed as in *Macginicarpa*, and the number of fruits per floret is only three to four (Pl. 34, figs. 10, 11, 13), rather than five. Anatomically, the achenes of *Tanyoplatanus* and *Macginicarpa* are very similar, with an endocarp of columnar sclereids, a mesocarp of angular parenchyma cells and a thin uniseriate cutinized exocarp (Pl. 34, fig. 15).

A single elongate staminate catkin (UF 9342) was recovered from the Nut Beds deposit that may also correspond to *Tanyoplatanus*. It has two stamens per floret with short filaments, capitate connectives and small tricolpate reticulate pollen.

Family **ROSACEAE** Juss.

The Rosaceae, or rose family, includes about 107 genera and 3000 species of trees shrubs and herbs. The family does not appear to be very important in the Nut Beds flora, being represented only by the genus *Prunus*. Two species of *Prunus* are recognized below on the basis of fruit types, and the same genus is also represented in the Nut Beds by silicified wood (E. Wheeler, pers. comm. 1991).

Genus **PRUNUS** L.

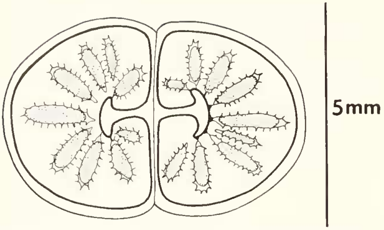
Prunus olsonii sp. nov.
Plate 35, figures 1–10

Etymology.—This species is named after Duane Olson, recognizing his help with field work in the Clarno Formation.

Description.—Fruit unilocular, single-seeded; endocarp pyriform, bilaterally symmetrical, rounded or rounded-truncate basally, tapering apically to an acute apex, with an apical keel in the plane of symmetry, length 6.6–6.8 mm, width 5.3–5.9 mm, thickness 4.5–5.3 mm, endocarp wall 0.35–0.65 mm thick, composed of, in succession: 1) a layer of fibers (five to eight cells and about 60 μm thick); inner part of the fibrous layer with fibers mostly oriented horizontally, the rest of the layer with fibers mostly oriented longitudinally, 2) the outer layer (0.2 mm) thick, composed of polygonal sclereids 125–550 μm in diameter with interspersed idioblasts about 20 μm in diameter, each with a single rhomboidal crystal. Locule cast similar in shape to the endocarp, smooth, usually with longitudinal raphe groove aligned with the apical keel, running from the apex to the chalazal truncation, length 5.8–6.0 mm, width 4.5–5.0 mm, thickness across plane of symmetry 4.1–4.3 mm. Seed coat forming a uniseriate layer of thin-walled rectangular cells 30 μm high and 50–90 μm wide.

Specimens.—Holotype: UF 9262, permineralized endocarp. Paratypes: UF 9748–9750, permineralized endocarps; UF 6460, 6461, USNM 354999, locule casts.

Discussion.—*Prunus olsonii* is represented by a few permineralized specimens and several locule casts. The locule casts show distinctive features such as pyriform shape (Pl. 35, figs. 1, 4), circular chalaza (Pl. 35, figs. 2, 3, 6, 7) and apical keel (Pl. 35, fig. 5). The main thickness of the endocarp is composed of sclereids with



Text-figure 15.—Transverse section of *Emmenopterys dilcheri* sp. nov., showing two carpellate fruit with seeds on axile placentae.

interspersed crystal-bearing idioblasts (Pl. 35, fig. 10). Prunoideae endocarps have a good fossil record in the European Tertiary (Mai, 1984), and have also been described from the Eocene Princeton chert of British Columbia (Cevallos-Ferriz and Stockey, 1991). Cevallos-Ferriz and Stockey (1991) recognized three types of *Prunus* endocarps from the Princeton chert which they named informally types 1 to 3. Similar idioblasts and crystals were described in the endocarp that they designated *Prunus* type 1 (Cevallos-Ferriz and Stockey, 1991).

Prunus weinsteinii sp. nov.

Plate 35, figures 11–15

Etymology.—This species is named after Michael Weinstein, recognizing his invaluable assistance with field work in the Clarno Formation.

Description.—Fruit unilocular, single-seeded, endocarp cherry pit-shaped, bilaterally symmetrical, elliptical in cross section, ovate in longitudinal view, with a longitudinal keel running along the margin in the plane of symmetry; base rounded, apex pointed; length 10.4 mm, width 8.6 mm, thickness 6.2 mm; surface gently rugulate; endocarp wall 0.8–1.2 mm thick, thickest in the region of the longitudinal keel, composed of polygonal, flat-sided, angular sclereids 25–38 μm in diameter (these cells becoming thinner walled and somewhat larger toward periphery) without obvious vascular bundles and with scattered idioblasts 20–30 μm in diameter each with a rhomboidal crystal; with an abscission/suture plane running from base to apex in the plane of symmetry along the ventral margin; a pair of vascular bundles straddling the abscission plane and running along the exterior of the endocarp; locule rounded, smooth lining. Seed coat with a thin uni-to biseriate outer layer 30 μm thick made up of horizontally elongate cells; preserved in dark color.

Specimen.—Holotype: UF 6800.

Discussion.—Although *Prunus weinsteinii* is known only from a single specimen, the anatomical preservation is excellent (Pl. 35, figs. 13–15). This species is distinguished from other unilocular fruits of similar size from the Nut Beds by the pronounced keel in the plane of symmetry and uniformity and compactness of the cells making up the endocarp. The restriction of the dehiscence plane to the ventral side (and absence on the dorsal side) is consistent with Prunoideae and distinguishes it from morphologically similar endocarps of Icacinaceae. This species differs from *P. olsonii*, treated above, by the larger size, thicker endocarp wall, and lack of the layer of fibers lining the locule. In overall shape, wall thickness and anatomy the endocarp closely matches that of domesticated cherry, *Prunus avium* (L.)L.

Family **RUBIACEAE** Juss.

The Rubiaceae are a large family of about 630 genera and 10,400 species of trees, shrubs, lianas and a few herbs. The family is distributed worldwide, especially in tropical to warm termperate settings. The fossil record of this large family is rather poorly known, but there are a few unequivocal records of the family in the Eocene of the northern Hemisphere, including the taxon described below.

Genus **EMMENOPTERYS** Oliv.

Emmenopterys dilcheri sp. nov.

Plate 36, figures 1–11; Text-figure 15

Etymology.—This species is named for David L. Dilcher, recognizing the importance of his contributions to angiosperm paleobotany.

Description.—Cymes with pedicellate, elongate fruits; infructescence axis at least 20 mm long, 0.5 mm thick, pedicels 8–10 mm long, with bract scars subtending each pedicel; fruits spindle-shaped, bilocular, septicidal multi-seeded capsules, fusiform in longitudinal view, circular to elliptical in cross section; base rounded-acute, tapering smoothly to the pedicel attachment, without a scar at the junction of the pedicel with the base of the fruit; apex acute, with short epigynous calyx; fruit length 15–20 mm, width measured perpendicular to the septum 6.2–7.0 mm, thickness in the plane of septum 3.6–4.0 mm; length/width ratio 2.5–2.8; exterior of fruit (exocarp?) smooth, with widely spaced longitudinal ribs; each carpel D-shaped in cross section, placentation axile, with a T-shaped placenta protruding nearly halfway into each locule; endocarp wall thin (approx. 0.125 mm), with transversely oriented fibers adjacent to locule; septum thin, approximately equal to thickness of endocarp wall; seeds numerous, imbricate, flattened and elongate parallel to the long axis of the fruit; seed ca. 3.0 mm long, 1.1–1.4 mm wide, 0.3–0.4 mm thick; consisting of an elliptical central body surrounded by a loosely adherent wing-like seed coat; seed coat with an outer layer of large cells 100–220 μm in diameter, four- to seven-sided in face view, with thick anticlinal walls but thin outer periclinal walls that are frequently collapsed; these cells reticulately thickened to form a grid of small polygonal depressions, 25–30 μm in diameter.

Specimens.—Holotype: OMSI Pb1197. Paratypes: OMSI Pb1307, UF 9333, 9494–9499, USNM 435091.

Discussion.—*Emmenopterys dilcheri* is represented by compressions of the infructescence (Pl. 36, fig. 1), and by casts and permineralizations of individual fruits. The holotype (Pl. 36, figs. 2, 3) shows the arrangement of fruits in the infructescence and, upon sectioning, revealed the bilocular structure and axile placentation (Pl. 36, figs. 4, 5). An especially well preserved isolated fruit was also sectioned (Pl. 36, fig. 6) to reveal details of seed position and morphology. The seeds, as seen in transverse (Pl. 36, figs. 7, 8) and longitudinal section (Pl. 36, figs. 9–11) show a distinctive seed coat of large reticulately thickened cells.

This species conforms to the Rubiaceae in the cymose infructescence, inferior ovary, bilocular fruit, axile placentation and endocarps with transversely arranged fibers. Capsular fruits occur in several tribes of the family (Schumann, 1891). Reticulately thickened, or "pitted" seed coats are characteristic of the subfamily Cinchonoideae (Bremekamp, 1966), and are considered to be plesiomorphic in the Rubiaceae because they also occur in Loganiaceae (Bremer and Struwe, 1992). The fossil is placed confidently in the tribe Cinchoneae (sensu Schumann, 1891) on the basis of pedicellate, elongate, thin-walled, septicidal capsules, with numerous tiny winged seeds (Standley and Williams, 1975). The Cinchoneae have about 40 genera occurring in tropical and subtropical regions. Genera with elongate, bilocular septicidal capsules particularly similar to the fossil include: *Badusa* (New Guinea, western Pacific), *Cosmibuena* (tropical America), *Emmenopterys* (China), *Exostema*, *Ferdinandusa* (tropical America), *Ladenbergia* (tropical America) and *Luculia* (Himalayas and Yunnan). These genera can be distinguished from one another by the size and extent of lobing of the persistent calyx and by features of seed morphology including size and shape of the wing, and the patterns of thickening of cells in the seed coat. The fossil most closely resembles extant *Emmenopterys*, to which it is assigned. *Emmenopterys dilcheri* compares well with extant *E. henryi*, a deciduous tree endemic to the mixed mesophytic forests of China, in the relatively inconspicuous persistent perianth, and in features of the seed including elongate wing shape (Pl. 36, fig. 12) and reticulate thickening of the seed coat cells (Pl. 36, fig. 13).

Emmenopterys dilcheri is the earliest record of fruits of Rubiaceae from North America. The same family has also been recognized on the basis of cuticularly preserved leaves from the middle Eocene Claiborne Formation of western Kentucky and Tennessee (Roth and Dilcher, 1979). Leaves of *Paleorubiaceophyllum* Roth et Dilcher (1979) have adnate stipules similar to those occurring in the genera *Condaminea* and *Cosmibuena* of the subfamily Cinchonoideae (tribes Condamineae and Cinchononeae, respectively). Taken together, these fruit and leaf records indicate that the subfamily Cinchonoideae of the Rubiaceae was well established in North America by the middle Eocene.

Family **SABIACEAE** Blume

The Sabiaceae are a family with three genera. *Sabia*, with about 20 species, is a genus of scandent shrubs, or rarely erect plants, distributed in eastern and southeastern Asia, Indomalesia and the Solomon Islands. *Meliosma*, distributed in Asia and central America, and *Ophiocaryon* of Central American distribution, are mainly trees and shrubs. *Meliosma* and *Sabia* are well represented in the fossil record of the northern hemisphere. The Sabiaceae are represented in the Nut Beds by several species of *Meliosma* and one of *Sabia*.

Genus **MELIOSMA** Blume

Meliosma is a genus of trees and shrubs found in the tropics and subtropics of eastern Asia, Malesia, Central America and the West Indies. It is well represented by endocarps in the late Cretaceous (Knobloch and Mai, 1986; Crane, Manchester and Dilcher, 1990, p. 32) and early Tertiary (Reid and Chandler, 1933; Mai, 1975; Crane et al., 1990) of Europe and North America. *Meliosma* is one of the most species-rich genera in the Nut Beds flora with five distinct species based upon fruits and seeds: *M. beusekomii* sp. nov., *M. bonesii* sp. nov., *M. elongicarpa* sp. nov., *M.* cf. *jenkinsii* Reid et Chandler, and *M. leptocarpa* sp. nov. In addition, the genus is represented at the same locality by leaves (Manchester, 1981) and wood (Manchester, unpublished). Leaves are reported from several other Tertiary localities in western North America (Taylor, 1990).

Van Beusekom (1971) emphasized the importance of endocarp characters in distinguishing extant subgenera, sections and species of *Meliosma*. Endocarps of *Meliosma* subgenus *Kingsboroughia* (Liebm.) Beus. are distinguished from those of subgenus *Meliosma* by the lack of a funicular canal within the endocarp. In subgenus *Kingsboroughia*, the vascular supply to the seed enters directly through a ventral pore in the endocarp, without passing through a funicular canal. Subgenus *Meliosma* is divided into two sections, *Meliosma* (Asian) and *Loranzanea* (Liebm.) Beus. (Central and South American), that can be differentiated by the morphology of the funicular canal morphology. In section *Meliosma*, the funicular canal is ventrally recessed within the endocarp, whereas in section *Lorenzanea*, the canal is ventrally extended. These differences are especially clear in longitudinal sections in the plane of symmetry as illustrated by Van Beusekom (1971, pp. 366–367, fig. 4), and are useful in the analysis of fossil remains (Pl. 38, figs. 1–4). According to these characters, the Nut Beds species correspond to subgenus *Kingsboroughia* (*M.* cf. *jenkinsii*), and to *Meliosma* subgenus *Meliosma*, section *Meliosma* (*M. beusekomii*, *M. bonesii*, *M. elongicarpa*, *M. leptocarpa*).

Subgenus MELIOSMA sensu Beus.

Section MELIOSMA sensu Beus.

Meliosma beusekomii sp. nov.

Plate 37, figures 1–5; Plate 38, figure 1;
Text-figure 16A

Etymology.—This species is named after C. F. Van Beusekom, recognizing the importance of his contributions to the systematics of *Meliosma*.

Description.—Endocarp subglobose, bilaterally symmetrical, obliquely truncate ventrally with a prominent circular funicular cavity or plug, and with a pronounced keel in the plane of symmetry; unilocular, single-seeded; dorsiventral height 3.2–5.7, avg. 4.2 mm (SD=0.61, n=31), length in plane of symmetry perpendicular to height 3.2–5.2, avg. 4.0 mm (SD=0.56, n-31), width across plane of symmetry 3.0–5.0, avg. 3.7 mm (SD=0.49, n=31); height/width ratio 1.1; gentle ridges on the lateral faces delimiting 5 to 10 facets or shallow depressions on each side of the median keel; lower lateral surface convex-rounded; funicular canal passing obliquely into the locule, 1.8 mm long; endocarp wall 0.4 mm thick, woody, composed of 10–12 rows of densely packed longitudinally elongate undulate-walled ("centipede-like") sclereids. Locule cast similar in shape to the endocarp, with more prominent, angular funicular cavity, and surface with small elongate punctae more or less aligned in vertical rows; seed conforming to the shape of the locule.

Specimens.—Holotype: UF 6673. Paratypes: HU 59978, UF 6672, 6683, 6674–6692, 6694–6705, USNM 435119 (lot of 60 specimens).

Discussion.—This is the most abundant species of *Meliosma* in the Nut Beds. It is represented by permineralized endocarps (Pl. 37, figs. 1–2; Pl. 38, fig. 1), and by locule casts (Pl. 37, figs. 3–5). The species is distinguished by facets or depressions on the lateral faces. The morphology of the endocarp wall in the funicular area, as seen in longitudinal section (Pl. 38, fig. 1; Text-fig. 16A) conforms to the pattern that Van Beusekom (1971) described as diagnostic for subgenus *Meliosma*, section *Meliosma*, and differentiates the species from the extant American section *Lorenzanea*. Among extant species, it is most similar in endocarp morphology to *M. simplicifolia* (Roxb.) Walp. and *M. pinnata* (Roxb.) Walp.

Meliosma bonesii sp. nov.

Plate 37, figs. 6–9; Plate 38, fig. 2;
Text-figure 16B

Etymology.—The epithet recognizes the major contributions of Thomas J. Bones through his persistent collecting at the Clarno Nut Beds locality.

Description.—Endocarp subglobose, bilaterally symmetrical, obliquely truncate ventrally with a prominent circular funicular cavity or plug and a pronounced median keel in the plane of symmetry; unilocular, single-seeded; dorsiventral height 3.8–7.6, avg. 5.5 mm (SD=1.34, n=7), length in plane of symmetry perpendicular to height 4.9–7.2, avg. 5.8 mm (SD=0.79, n=7), width across plane of symmetry 4.6–7.5, avg. 5.7 mm (SD=0.93, n=7); height/width ratio 0.8–1.0; lateral faces smooth and rounded; lower lateral surface more or less straight; funicular canal passing obliquely into the locule, 3.2 mm long; endocarp wall 0.6 mm thick, woody, composed of elongate sinuous-walled sclereids. Locule cast with more prominent, angular funicular cavity, and surface with small elongate punctae more or less aligned in vertical rows.

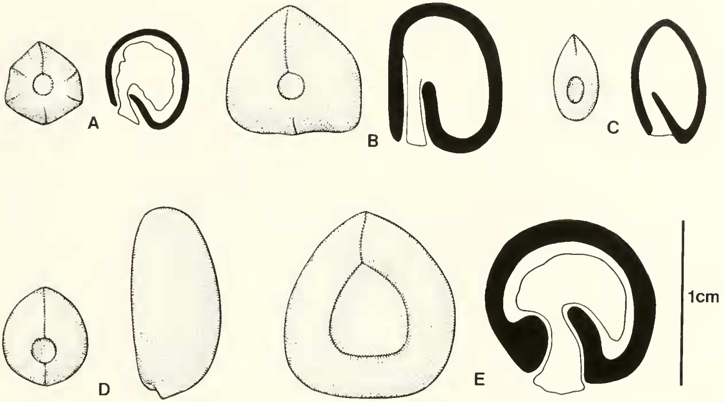
Specimens.—Holotype: UF 6714. Paratypes: UF 6712–6717, 6802, 6803, 6811–6816, 6825–6833.

Discussion.—*Meliosma bonesii* is represented by permineralized endocarps (Pl. 37, figs. 6, 7) and locule casts (Pl. 37, figs. 8, 9). Endocarps of this species tend to be larger than those of *M. beusekomii*, but there is some overlap in size range. Morphologically, *M. bonesii* is distingished from *M. beusekomii* by smooth, rounded, rather than faceted lateral faces, and by the more or less straight rather than convex basal side. Longitudinal sections in the plane of symmetry show a well-developed oblique funicular canal (Pl. 38, fig. 2; Text-fig. 16B) with morphology conforming to that indicated of subgenus *Meliosma*, section *Meliosma* (Van Beusekom, 1971). *M. bonesii* shows thicker walls and a more elongate locule) than *M. beusekomii* (cf. Text-figs. 16B and 16A).

Meliosma elongicarpa sp. nov.

Plate 37, figures 10–12; Text-figure 16D

Etymology.—*elongatus* (L = prolonged) + *karpos* (Gr = fruit), referring to the elongate form of the endocarp.



Text-figure 16.—*Meliosma* species from the Nut Beds. **A**, *Meliosma beusekomii* sp. nov., ventral view and longitudinal section in plane of bisymmetry showing oblique funicular canal. **B**, *M. bonesii* sp. nov., ventral view and longitudinal section in plane of bisymmetry. **C**, *M. leptocarpa* sp. nov. ventral view and longitudinal section in plane of bisymmetry. **D**, *M. elongicarpa* sp. nov., ventral and lateral views. **E**, *M.* cf. *jenkinsii* Reid et Chandler, ventral view and longitudinal section in plane of symmetry.

Description.—Endocarp elongate-ellipsoidal, bilaterally symmetrical, with circular ventral funicular plug, and with a median keel in the plane of symmetry, unilocular, single-seeded; dorsiventral height 9.8 mm, length in plane of symmetry perpendicular to height, 5.0 mm, width across plane of symmetry 4.4 mm, height/width ratio 2.2; lateral faces smooth and rounded; lower lateral side convex, rounded; funicular canal passing obliquely into the locule.

Specimen.—Holotype: UCMP 10701.

Discussion.—This species, known only from a few specimens, is distinguished from the other Clarno species by its elongated height, which results in a height/width ratio of about 2; the other species have height/width ratios of about 1. The morphology is consistent with placement in section *Meliosma*. Larger, but similarly elongate endocarps occur in extant *M. sumatrana* (Jack) Walp. of Sumatra.

Meliosma leptocarpa sp. nov.

Plate 37, figures 16–19; Plate 38, figure 4;
Text-figure 16C

Etymology.—*Leptos* (Gr = thin, slender) + *carpum* (Gr = fruit) referring to the narrow width of the endocarps.

Description.—Endocarp ellipsoidal, bilaterally symmetrical, laterally compressed in the plane of symmetry; with a pore on the ventral surface, finely rugulate, with a median keel running all around the endocarp in the plane of symmetry; unilocular, single-seeded, dorsiventral height 4.0–5.1, avg. 4.6 mm (SD=0.36, n=17), length in plane of symmetry perpendicular to height 2.8–4.5, avg. 3.4 mm (SD=0.52, n=17), width across plane of symmetry 2.0–2.6, avg. 2.2 mm (SD=0.18, n=17); height/width ratio 1.8–2.4, surface rugose; endocarp wall 200 μm thick, composed of longitudinally elongate "centipede-like" cells. Locule casts similar in shape to the endocarps, but smooth-surfaced, height 2.8–5.0, avg. 4.0 mm (SD=0.50, n=16), length 2.5–4.0, avg. 3.0 mm (SD=0.34, n=16), width 1.5–2.3, avg. 2.0 mm (SD=0.17, n=16).

Specimens.—Holotype: UF 6725. Paratypes: UF 6739–6768, 6817–6819, USNM 355377 (8 specimens), 355430, 355435 (10 specimens), endocarps.

Discussion.—This species is very common in the Nut Beds. It is distinguished by its very narrow width and prominent surface ruminations of the endocarp. At first I was hesitant to place this species in *Meliosma*, because the endocarps are more compressed in the plane of symmetry than any other extant or fossil species of the genus. However, longitudinal sections (Pl. 38, fig. 4; Text-fig. 16C) reveal internal morphology and anatomy diagnostic of *Meliosma* and funicle as in other species of *Meliosma*. The morphology of the endocarp wall in the funicular area, as seen in longitudinal section, indicates that this species conforms to the Asian section *Meliosma*.

Subgenus **KINGSBOROUGHIA** sensu Beus.

Section **KINGSBOROUGHIA** sensu Beus.

Meliosma cf. **jenkinsii** Reid et Chandler

Plate 37, figures 13–15; Plate 38, figure 3;
Text-figure 16E

Description.—Endocarp large, subglobose, bilaterally symmetrical, smooth, ventral side marked by a prominent rounded triangular funicular plug; with a pronounced median keel in the plane of symmetry; unilocular, single-seeded; dorsiventral height 8.0–13.2, avg. 11.4 mm (SD=1.8, n=7), length in plane of symmetry perpendicular to height, 8.5–13.2, avg. 11.0 mm (SD=1.7, n=7), width across plane of symmetry 9.0–12.2, avg. 10.4 mm (SD=1.4, n=7), height/width ratio 0.9–1.0; endocarp wall 0.8–1.0 mm thick, woody, composed of elongate undulating cells. Locule cast conforming in shape to the endocarp, smooth, rounded, with prominent ventral cavity and pronounced median keel, height 9.0–11.4, avg. 10.4 mm (SD=1.2, n=7), length 7.4–11.5, avg. 9.9 mm (SD=1.5, n=7), width 7.8–11.3, avg. 9.2 mm (SD=1.6, n=7).

Specimens.—UF 6706, 6707, 6786, 9405, 9851, USNM 355193, 435084, 446060, 446065, 446059.

Discussion.—*Meliosma* cf. *jenkinsii* is distinguished from other Clarno species of *Meliosma* by its larger size, smooth contours and more massive ventral plug. The funicular canal is short, and not markedly oblique. The species is represented by a single complete endocarp and several locule casts, some with patches of the endocarp wall remaining. The range of endocarp size was extrapolated by adding the thickness of the endocarp wall (0.9 mm × 2) to the locule cast dimensions.

This species corresponds in size and shape to *Meliosma jenkinsii* Reid et Chandler from the London Clay (Reid and Chandler, 1933; Chandler, 1961b), and Geiseltal (Mai, 1975) floras. Van Beusekom (1971) states that the fossils "should undoubtedly be placed in Subgenus *Kingsboroughia* Section *Kingboroughia* by the fact that the vascular bundle running through the ventral pore of the endocarp wall is situated in a ventral groove in the latter, and is still present in the shape of a spatulate ventral 'plug' at the ventral side of the endocarp." Longitudinal sections of the Clarno specimens support Van Beusekom's conclusion (Pl. 38, fig. 2; Text-fig. 16E). *Meliosma* Section *Kingsboroughia* is disjunct today between central America and Asia with two species, *M. alba* and *M. rufo-pilosa*.

Genus **SABIA** Colebr.

Sabia prefoetida (Becker) comb. nov.

Plate 38, figures 5–8

Symplocarpus prefoetidus Becker, 1969, p. 10, pl. 13, figs. 19, 20.
Sabia, Bones, 1979, pl. 3, fig. 14.

Description.—Endocarp unilocular, single-seeded, laterally compressed, bilaterally symmetrical, resembling a painter's pallete in lateral view, rounded in lateral outline except for a ventral notch containing the funicle; length (longest dimension) 3.3–5.5, avg. 4.5 mm (SD=0.55, n=11), width across plane of symmetry 1.1–1.6, avg. 1.4 mm (SD=0.15, n=11), height (at right angle to length) 3.1–4.8, avg. 4.1 mm (SD=0.40, n=11); keel in the plane of symmetry running from the basal scar nearly 320° around the fruit terminating in a sharp rostrum adjacent to the ventral notch, both lateral faces with about 30 shallow crater-like depressions, which are largest in the center, decreasing in size toward periphery.

Specimens.—HU 59977, 59989, UCMP 10652–10654, UF 5245, 6727–6736, 6801, 6822–6824, USNM 353968. Holotype: YPM-NYBG 894 from Beaverhead Basin, Montana.

Discussion.—*Sabia* is represented in the Nut Beds by endocarp and locule casts. Although no cellular details are preserved, the shape, size and surface sculpture of these casts correspond closely to extant *Sabia*. The size and sculpture correspond very closely to the endocarp impressions that Becker (1969) illustrated from the Christensen Ranch locality of the Beaverhead basin of southwestern Montana. Reexamination of Becker's original specimens, now at Yale University, has confirmed that they are endocarp impressions having nothing to do with the spadices of *Symplocarpus*. *Sabia* has a good fossil record in Europe, ranging from the late Cretaceous of Czechoslovakia and Germany (Knobloch and Mai, 1986), to the Miocene of Poland (Czeczott and Skirgiello, 1959) and Germany (Gregor, 1978) to the Pliocene of France (Geissert and Gregor, 1981).

Family **SAPINDACEAE** Juss.

The Sapindaceae are a large family of 144 genera and 1325 species of tropical to temperate trees, shrubs, lianas and herbaceous climbers. Fruits of Sapindaceae range from berries to samaras (Van Welzen, 1988). Seeds of the family are exalbuminous, with highly characteristic embryos that completely fill the seed. Reid and Chandler (1933) observed that "the curved, tapering radicle, sometimes large, sometimes small, is contained in a pocket of the seed coat. The large cotyledons may lie upon or beside one another, and be without folds; or they may lie upon one another and be folded or coiled together in a more or less complicated manner." Because the superficial characters of the embryo are impressed more or less distinctly on the inner surface of the seed coat, these characters may also be observed in fossil seeds.

The Sapindaceae are represented in the Nut Beds by three taxa: *Deviacer wolfei* gen. et sp. nov., and two species of *Palaeoallophylus*. Elsewhere in the Clarno Formation, the family is represented by impressions of the distinctive bladder-like fruits of *Koelreuteria* (Sheep Rock Creek locality, Manchester, unpublished). The Aceraceae, which logically should be treated as a tribe within Sapindaceae (Radlkofer, 1890; Muller and Leenhouts, 1976), have not been identified among the Nut Beds fruits and seeds, although *Acer* fruits occur at the Sheep Rock Creek locality of the Clarno Formation (Wolfe and Tanai, 1987), and fruits of *Dipteronia* occur at the Sheep Rock Creek, Dry Hollow, and White Cliffs localities.

Genus **DEVIACER** gen. nov.

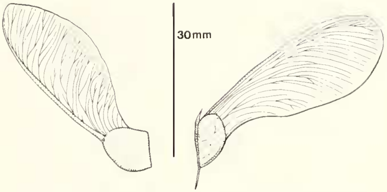
Etymology.—*Devius* (L = turn or bend aside; deviate) + *Acer* (L = maple), referring to the backward orientation of the fruits with respect to those of *Acer*.

Type species.—*Deviacer wolfei* sp. nov.

Deviacer wolfei sp. nov.
Plate 39, figures 1–6; Text-figure 17B

Etymology.—The epithet is in honor of Jack A. Wolfe recognizing his contributions to paleobotany and the systematics of Sapindales.

Description.—Samara bilaterally symmetrical, with an elongate lateral wing in the plane of symmetry adjoining an elliptical nutlet; samara length 20–34, avg. 24 mm (SD=4.7, n=8), width 5.0–10.3, avg. 7.7 mm (SD=1.8, n=8); pedicel/stipe (proximal keel) 3–4 mm long, without obvious perianth scars; nutlet elliptical, length 5.0–8.0, avg. 6.2 mm (SD=1.8, n=7), width 2.2–4.5, avg. 3.2 mm (SD=0.82, n=7), up to about 2.5 mm thick with reticulate ribbing pattern over the surface, rounded laterally except for a flattened abscission scar on the dorsal margin; this scar oriented at 40–60° to the trend of the wing; wing dorsal margin more or less straight to slightly convex, rounded distally; ventral margin concave proximally forming a sulcus adjacent to the nut, convex, rounded distally; venation subparallel, dichotomizing, running parallel to the dorsal margin for some distance then arching distally toward the ventral margin; veins closer together and coalesced along the straight dorsal margin of the wing; a rudder-like projection 1.0–1.2 mm long arises from the nut opposite the pedicel attachment and protrudes parallel to the long axis of the seed, with its tip recurved toward the wing.



Text-figure 17.—Comparison of *Acer* and *Deviacer* samaras. **A**, *Acer grandidentatum*. **B**, *Deviacer wolfei* gen. et sp. nov.

Specimens.—Holotype: OMSI Pb1133. Paratypes: OMSI Pb489, 567, 590, 632, 633, 634, 638, 724, 802, 930, 1107, 1110, 1117, 1124, 1129, 1130, 1321, 1325, 1425, 1521, 1524, 1529, 1576, 1593, 1594, 1774, 1786.

Discussion.—*Deviacer* is common at the Nut Beds in a small area of the basal leaf layer at the north end of Face 3, preserved as impressions showing good details of the venation (Pl. 39, figs. 1–5). It is also known from impressions at other Clarno localities including West Branch Creek, White Cliffs (Pl. 39, fig. 6) and Gosner Road. This material appears to be conspecific with that from the middle Eocene of British Columbia attributed to *Acer* sp. by Mathewes and Brooke (1971).

Referring to this type of samara informally as the "*Acer*" *arcticum* type, Wolfe and Tanai (1987) pointed out that it may represent an extinct genus of Aceraceae. The samaras resemble those of *Acer* in shape of the seed, the coarse reticulum of veins over the nutlet, and in the shape and venation of the wing (Pl. 39, figs. 1–6), yet they differ fundamentally in mode of attachment. Whereas in *Acer* the attachment scar is situated on the ventral margin of the nutlet and forms an acute angle with the thickened margin of the wing (Text-fig. 17A), in *Deviacer* the scar is on the dorsal margin of the nutlet and forms an obtuse angle with the thickened lateral margin of the wing (Text-fig. 17B). The large flat attachment scar indicates that the fruits were schizocarpic, with two or more fruits sharing the same axis, as in fruits of *Acer*. In *Acer* schizocarps the ventral wing margins of adjoining samaras face each other. Although fruits of *Deviacer* have not been found in connection, the attachment angle indicates that the dorsal margins of the wings would have faced each other. As noted by Wolfe and Tanai (1987), this orientation is encountered among extant samaroid Sapindaceae; however, "in samaroid Sapindaceae (primarily Paullinieae), the samaras are typically attached along the length of the wing (as well as along the nutlet) and the veins are not strongly coalesced along one side of the wing; this last character is valid also for sapindaceous samaras that are attached only along the nutlet."

It is not known whether *Deviacer* samaras were borne in pairs as in Aceraceae or in threes as is typical of Sapindaceae. Although the family name Aceraceae is well ingrained in the literature, there is no firm basis for treating it separately from the Sapindaceae. Radlkofer (1890) concluded on macromorphological grounds that the Aceraceae should logically be treated as a tribe within Sapindaceae, an interpretation that is also supported on the basis of pollen morphology (Muller and Leenhouts, 1976). *Deviacer* is thus treated as an extinct genus of Sapindaceae sensu lato.

Genus **PALAEOALLOPHYLUS** Reid et Chandler

The generic name *Palaeoallophylus* denotes similarity in pattern of folding of the embryo to that seen in extant *Allophylus*. However, as noted by Reid and Chandler (1933) when they established this genus, similar patterns of embryo folding may occur in other extant genera of this large family. Although assignment of these fossils to the Sapindaceae is sound, other characters would be needed to determine how closely the fossil is allied to extant *Allophylus*.

Palaeoallophylus globosa sp. nov.

Plate 38, figures 9, 10

Description.—Seed globose, bilaterally symmetrical, with a large folded and coiled embryo; length 3.6–6.0, avg. 4.6 mm (SD=0.52, n=30), width 3.7–5.2, avg. 4.5 mm (SD=0.45, n=29), thickness (3.2) 3.5–5.2, avg. 4.1 mm (SD=0.55, n=29). Length/thickness ratio 0.8–1.2; hilar scar medial, adjacent to radical; seed coat smooth, thin (0.1–0.2 mm), forming a pocket around the radical ¾ as long as the seed; chalaza marked by a transverse band inside the seed coat situated about ¼ of the circumference from the hilum; seed exalbuminous, embryo large, consisting of two cotyledons folded one inside the other like a bent knee, encircled by a coil of the hypocotyl and radicle; radicle tapering laterally.

Specimens.—Holotype: UF 6587. Paratypes: HU 59965, OMSI Pb194, UF 6585, 6586, 6589–6595, USNM 312766 (Bones, 1979, pl. 4, fig. 1), 355041–355043, 355046, 355055, 355058, 355059, 424852–424857, 424859–424871.

Discussion.—*Palaeoallophylus globosa* is represented by internal molds of the seed coat; usually the seed coat itself is not preserved except in the radicle region. These molds clearly show the impression made by the large folded and coiled embryo (Pl. 38, figs. 9, 10). The combination of a coiled embryo and a pocket in the seed coat containing the radicle is characteristic of extant and fossil Sapindaceae as noted by Reid and Chandler (1933). This species is similar in shape, but somewhat smaller than *Palaeoallophylus rotundatus* Reid et Chandler from the London Clay flora (Reid and Chandler, 1933).

Palaeoallophylus gordonii sp. nov.

Plate 38, figures 11–16

Etymology.—This species is named for Ian Gordon, who provided extensive help with paleobotanical field work in the Clarno Formation.

Description.—Seed elongate ovoid, bilaterally symmetrical, rounded apically and truncate to obtuse-conical at the hilar end; length 4.8–6.0, avg. 5.4 mm (SD=0.44, n=13), width 3.3–4.9, avg. 4.1 mm (SD=0.43, n=13), thickness 3.2–4.5, avg. 3.6 mm (SD=0.43, n=13), length/thickness ratio 1.3–1.8; seed coat 75–100 μm thick, smooth, forming a pocket around the radicle about ⅔ of the length of the seed; seed exalbuminous, embryo large, consisting of two cotyledons folded one inside the other in an "S" configuration; radicle tapering toward the hilum.

Specimens.—Holotype: USNM 424669. Paratypes: UCMP 10730, 10731, UF 6584, 6596, 6597, USNM 355048, 355051 (10 specimens), 355060, 424666–424668, 424670.

Discussion.—This species is represented by internal molds of the seed coat, showing the impression of the folded cotyledons and the protruding radicle (Pl. 38, figs. 11, 12), sometimes with remains of the seed coat adhering (Pl. 38, figs. 13–16). The seeds of this species are narrower, more elongate, than those of *P. globosa*. It is similar in morphology, but somewhat smaller than *Palaeoallophylus minimus* Chandler (1961b; = *Sapindospermum* sp. 4, Reid and Chandler, 1933) from the London Clay.

Family **SAPOTACEAE** Juss.

The Sapotaceae are a family of about 107 extant genera and 1000 species of trees and shrubs, mostly tropical in distribution. The seeds described below confirm the presence of this family in the Nut Beds.

Genus **BUMELIA** Sw.?

Bumelia? globosa sp. nov.

Plate 39, figures 7–16

Description.—Seed anatropous, subglobose; internal mold of seed coat bilaterally symmetrical, circular in cross section, slightly longer than wide, with an oblique, apical truncation, base rounded to slightly pointed; length 3.3–5.9, avg. 4.5 mm (SD=0.49, n=25), equatorial diamter 3.2–4.4, avg. 3.9 mm (SD=0.25, n=25);

truncate face flat, circular in outline, perpendicular to the plane of symmetry, sloping toward the front of seed at 70° to the long axis of the seed; hilum a small scar near the center of the truncation, slightly offset toward the edge along which the raphe travels; micropyle evident as a tiny pore at the highest end of the truncation; raphe bundle passing in the plane of symmetry from the hilum across the front margin of seed to the chalaza at the base; with a network of veins radiating from the hilum over the truncate surface.

Specimens.—Holotype: USNM 424644. Paratypes: HU 60000, UCMP 10645–10649, UF 8668, 8669, 8672–8685, USNM 353964 (21 specimens), 353965 (4 specimens), 355446, 355488 (6 specimens), 424656–424664.

Discussion.—This species is represented by translucent chalcedony internal molds of the seed coat. The raphe is sometimes preserved as an opaque band that can be observed in silhouette within the translucent chalcedony (Pl. 39, fig. 10). The seed coat itself is not preserved.

The morphology of these specimens closely matches that of the cavity inside the hard seed coat of extant *Bumelia lacuum*. They correspond in size, bisymmetry, angle of the truncation, the nearly hemispherical, but subtly pointed base, relative spacing of the hilum and micropyle, course and thickness of the raphe. Because the Nut Bed fossils are missing the seed coat, the resemblance of these fossils to seeds of extant *Bumelia* is not immediately obvious. However, if a mold were to be made of the inside of the seed coat of an extant seed, it would be difficult to distinguish from these fossils. The assignment to *Bumelia?* includes a question mark because my study of extant seeds in this family has not been sufficiently thorough to establish that the morphology of these seeds is unique to that genus.

Bumelia? **subangularis** sp. nov.

Plate 39, figures 17–21

Etymology.—The epithet refers to the subangular external morphology of the seed.

Description.—Seed subellipsoidal, bilaterally symmetrical, smooth, obliquely truncate apically, rounded basally, rounded-subtriangular outline in cross section; length 6.0–6.9, avg. 6.6 mm (SD=0.43, n=5), width across plane of symmetry 3.7–5.0, avg. 4.6 mm (SD=0.54, n=5), width parallel to plane of symmetry 4.0–5.4, avg. 4.6 mm (SD=0.55, n=5); truncation more or less flat, obovate in outline, sloping toward front of seed at 50–60° to the long axis of the seed, circular hilar scar in the center of the truncation; network of veins radiating from the hilum in plane of truncation.

Specimens.—Holotype: UF 8743. Paratypes: UF 8744, USNM 424681, 435082, 435083.

Discussion.—This species is represented by chalcedony seed casts without internal structure preserved. The smooth, shiny surface of the fossils suggests that the seeds were hard and shiny, possibly from a bird-dispersed berry. The slight angling (Pl. 39, figs. 17, 18) suggests that more than one seed may have been present in each fruit. Because of the subangular morphology and larger size, *Bumelia? subangularis* is interpreted to be a different species from the globose internal molds of seed coat described above as *B.? globosa*.

Family **SCHISANDRACEAE** Bl.

The Schisandraceae contains two extant genera of tropical to warm temperate climbing shrubs: *Schisandra* and *Kadsura*. *Schisandra* is distributed in Asia (24 species) and eastern North America (one species); *Kadsura* (22 species) is distributed from India to Malesia. The two genera are similar in most vegetative and reproductive characters but are distinguished on the basis of a simple difference in infructescence morphology (Smith, 1947). The berries of *Kadsura* are borne together in a globose head, whereas those of *Schisandra* occur separated on an elongate spike. Seeds of both genera are campylotropous and shallowly c-shaped, with a thin, hard seed coat, cellular endosperm and small embryo.

Genus **SCHISANDRA** Michx.

Schisandra oregonensis sp. nov.

Plate 40, figures 1–11

Schisandraceae, Bones, 1979, pl. 1, fig. 8.

Etymology.—The epithet refers to Oregon.

Description.—Seed reniform to cashew-shaped, curved in plane of bisymmetry, rounded at both ends; length 3.7–9.9, avg. 5.6 mm (SD=1.9, n=22), dorsiventral width 3.0–7.5, avg. 4.5 mm (SD=1.4, n=22), thickness across plane of symmetry 1.9–5.0, avg. 2.9 mm (SD=0.88, n=22); surface smooth; hilum situated in the ventral sinus; raphe originating at the hilum and running a medial course along the dorsal curve, diminishing in prominence toward the micropylar end; outer surface (rarely preserved) with small craters; inner layer of seed coat smooth. Seed coat composed of: 1) an inner uni- to biseriate layer of mostly isodiametric cells 20–30 μm in diameter, 2) a prominent uniseriate layer of anticlinally oriented thin-walled columnar cells 100–130 μm high, 40–65 μm wide, 3) a 3- to 5-seriate layer of polygonal cells, sometimes periclinally elongate, 50–150 μm wide and 30–45 μm high, which proliferates to form a thick layer of isodiametric cells in the hilar sinus.

Specimens.—Holotype: USNM 424655. Paratypes: OMSI Pb1855, UCMP 10630, UF 6576, 6577, 6579–6583, USNM 312771 (Bones 1979, pl. 1, fig. 8), 355061 (6 specimens), 355654 (3 specimens), 355061 (6 specimens), 424654 (3 specimens), 424732, 424809.

Discussion.—*Schisandra* is represented by chalcedony casts, molds and permineralized specimens. Conspicuous features of these seeds are the curvature, dorsal raphe (Pl. 40, figs. 5, 7), and the thick uniseriate columnar layer of the inner seed coat (Pl. 40, figs. 9–11).

Seeds of Shisandraceae are bitegmic (Kapil and Jalan, 1964; Corner, 1976) and the inner part of the seed including the tegmen (inner seed coat) may become loose within the testa (outer seed coat) at maturity (Pl. 40, figs. 14–18). Most of the fossil specimens are molds or permineralizations of the inner part of the seed, including the tegmen but excluding part of the testa. These have a smooth surface and a well developed hilar sinus and evidently were formed as infillings of the testa. External seed morphology is revealed in a rare chalcedony cast of a complete seed with the testa intact (Pl. 40, fig. 1), showing a rough, minutely cratered external surface, and a thick, lip-like rim along the hilar sinus.

These seeds resemble those of both *Kadsura* and *Schisandra* in size, reniform shape, dorsal raphe, and seed coat anatomy. The uniseriate columnar layer of the tegmen, and the proliferation of isodiametric testa cells in the hilar region observed in the fossil specimens are similar to those of extant seeds. The seed surface is smooth in all extant species of *Kadsura* and in some extant species of *Schisandra* (Pl. 40, fig. 12), but rough-surfaced seeds occur only in *Schisandra* (Pl. 40, fig. 13). The latter feature provides support for assignment of the fossil to *Schisandra* rather than *Kadsura*. The seed size of this *Schisandra oregonensis* is variable, such that the largest specimens are about twice as big as the smallest ones. Dimensions may have varied with the number of seeds per berry; there may be from one to five seeds in berries of extant species.

Although *Schisandra* has one extant species in eastern North America, the Clarno occurrence is the only known North American fossil record. The genus has also been determined on the basis of cuticularly preserved leaves from the Eocene Geiseltal flora of Germany (Jähnichen, 1976) and on the basis of seeds from the Pliocene of Alsace, France (Gregor, 1981).

Family **STAPHYLEACEAE** Lindley

The Staphyleaceae are a family of five genera and about 50–60 species of trees and shrubs, of tropical to temperate distribution in the northern hemisphere. The family is divided into two subfamilies: Staphyleoideae (*Euscaphis*, *Staphylea*, *Turpinea*) and Tapiscioideae (*Tapiscia*, *Huertea*). Both subfamilies are well represented in the Tertiary of Europe and North America (Mai, 1976; Tiffney, 1979; Manchester, 1988). The family is represented in the Nut Beds by fruits and seeds of *Tapiscia*.

Genus **TAPISCIA** Oliver

Tapiscia occidentalis Manchester 1988
Plate 41, figures 1–9

Tapiscia occidentalis Manchester, 1988, p. 59–66, figs. 1–11, 18, 20.

Description.—Fruit subglobose, rounded apically, tapered basally to a point with a circular pedicel scar 0.4–0.5 mm in diameter; fruit length 5.0–5.8, avg. 5.4 mm (SD=0.40, n=6), width 4.0–4.5, avg. 4.2 mm (SD=0.20, n=6), thickness 3.2–4.3, avg. 3.7 mm (SD=0.40, n=6), pericarp thin (<0.2 mm) following the form of the anatropous seed; endocarp surface with small, regularly spaced scabrae; internal cast of seed-coat subglobose, length 3.7–5.4, avg. 4.6 mm (SD=1.12, n=18), width 3.0–4.5, avg. 3.7 mm (SD=0.40, n=18), thickness 2.5–4.1, avg. 3.2 mm (SD=0.47, n=8); bisymetrical, rounded dorsally, pointed at the micropylar end, and concave ventrally with a prominent circular chalazal scar 1.5–2.5 mm in diameter, surface smooth to finely striate with striae running longitudinally on the dorsal surface and radiating all directions from the chalaza on the ventral surface; seed coat 180 μm thick, composed of five to six layers of anticlinally aligned elongate cells 12.5–20 μm wide, 25–90 μm high.

Specimens.—Holotype: UF 5200, cast of a fruit with outer layer partially broken away revealing internal seed cast. Additional specimens: UF 5201, 5202, 6511, 9283, 9284, 9692, 9718–9720, USNM 354498, complete fruits; HU 59975, 59927, UCMP 10678–10686, UF 5203–5220, 9721 (20 specimens), USNM 312767 (Bones, 1979, pl. 6, fig. 2), 355449–355451, 355453, 355454 (9 specimens), 355455 (8 specimens), 355457 (6 specimens), 435004 (Bones, 1979, pl. 6, fig. 1), seed casts.

Discussion.—*Tapiscia occidentalis* was originally described from fruit and seed casts without cellular detail (Manchester, 1988). Some permineralized specimens have since been recovered (Pl. 41, figs. 4, 7–9), providing the anatomical details included in the above description, and confirming the assignment to *Tapiscia*. The species was identified through comparison with fruits and seeds of extant Tapiscioideae, i.e., *Tapiscia sinensis* Oliver, *Huertea cubensis* Griseb., and *H. granadina* Cuatrec. The fossil conforms to *Tapiscia* in its small size, uneven tegmen thickness, regularly spaced bumps on the outer surface, and the typically acute micropyle.

Fossil seeds of Tapiscioideae also occur in the Eocene Geiseltal flora of Germany (Mai, 1976). From the London Clay flora, Mai recognized three species of *Tapiscia* previously designated *Carpolithes pusillus* (Reid et Chandler) Chandler (1961b). Mai (1980) recognized a fourth species from the middle Eocene Geiseltal flora of Germany and provided a key for the identification of the five European *Tapiscia* species using size, shape (elongate vs. rounded), ornamentation, and prominence of micropyle as diagnostic characters. *Tapiscia occidentalis* is very close in morphology to *T. pusilla* from the London Clay. Both species share the same shape and external ornamentation with both having a pointed micropyle. The only difference seen between the two species is slightly larger size of *T. occidentalis* specimens.

Tapiscia has a single living species that is a small tree up to 10 m high growing in the mixed mesophytic forests of the Yangtze-Kiang valley between Yunnan, western Szechuan, Hupeh and northern Chekiang in China (Wang, 1961). It is also recorded from wet forests to 1600 m in Kwangtung and Tonkin, China (Krause, 1942).

Family **SYMPLOCACEAE** Desf.

The Symplocaceae are a family of one genus, *Symplocos*, with about 250 species of trees and shrubs distributed in new world and old world tropics excluding Africa, and extending into temperate North America. Old world Symplocaceae have been monographed with attention to fruits and other characters by Nooteboom (1975). Those of the Antilles have been revised with attention to many of the same characters by Mai (1986). Nooteboom (1975) considered the morphology of fruits and of endocarps to be taxonomically useful for groups of species, but refrained from making a key to individual species based solely on fruit characters. *Symplocos* has an excellent fossil fruit record in Europe, extending from the Eocene (Reid and Chandler, 1933; Chandler, 1961b) to the late Pliocene (Kirchheimer, 1957), as reviewed in detail by Mai (1970). The following constitutes the first fossil fruit record of the genus described from North America and is complementary to previous records based upon fossil pollen (Taylor, 1990). *Symplocos* fruits are also known on the basis of an underscribed species from the Brandon lignite of Vermont (Tiffney, pers. comm., 1992).

Genus **SYMPLOCOS** Jacq.

Symplocos nooteboomii sp. nov.

Plate 41, figures 10–17

Etymology.—This species is named in recognition of the important studies of extant *Symplocos* carried out by H. P. Nooteboom.

Description.—Endocarp ovoid or ellipsoidal, somewhat compressed laterally, slightly flared and transversely truncate apically, rounded or obtusely pointed basally; length 8.6–15.2, avg. 11.3 mm (SD=3.48, n=3), width 6.1–11.2, avg. 8.3 mm (SD=2.14, n=4), thickness 5.4–6.9, avg. 6.1 mm (SD=0.67, n=4); with 13–14 unbranched meridional grooves or ribs (depending on preservation) radiating from the base and extending to the apical truncation; four or five locules indicated by distinct pores in the apical truncation.

Specimens.—Holotype: USNM 354596. Paratypes: USNM 354592, 354602, 354603.

Discussion.—Only a few specimens of *Symplocos* are known from the Nut Beds. They are preserved as chalcedony casts, without anatomical preservation. Endocarps of this genus are so distinctive morphologically, however, that cellular details are not required for identification. Assignment to *Symplocos* is based on the combination of meridional grooves, ovoid shape (Pl. 41, figs. 10, 11), and the truncate apex with openings corresponding to each of the locules (Pl. 41, figs. 12, 13, 15). The apical truncation apparently corresponds to the base of the calyx as in the extant genus. Extant species of *Symplocos* have fruits that range in length from a few millimeters to about four centimeters and may have from one to five locules (Nooteboom, 1975).

Family **THEACEAE** D. Don

The Theaceae, or tea family, is a family of about 28 genera and 520 species of trees, shrubs and occasional lianas, chiefly of tropical distribution but with a few warm temperate representatives. The family is known from well-preserved fruits in the Eocene of Tennessee and Kentucky (Grote, 1989; Grote and Dilcher, 1989) and in the Tertiary of Europe (Mai, 1971). The fossil record of Theaceae in the northern hemisphere is reviewed by Grote and Dilcher (1989). *Cleyera* is the only genus of this family that has been confirmed among the Nut Beds seeds.

Genus **CLEYERA** Thunb.

Cleyera grotei sp. nov.

Plate 42, figures 1–5

Etymology.—This species is named after Paul J. Grote, recognizing his contributions to the fossil history of the Theaceae.

Description.—Seed campylotropous, laterally flattened, rounded in outline, truncate at micropyle and chalaza end, with a medial condylar depression on both faces of the seed, around which the c-shaped embryo cavity curves; length 1.5–2.3, avg. 1.8 mm (SD=0.22, n=14), width 1.4–2.0, avg. 1.8 mm (SD=0.15, n=14), thickness 0.6–0.9, avg. 0.7 mm (SD=0.08, n=14); outer surface reticulate with thick walled cells 100–200 μm in diameter arranged in more or less concentric rows, these cells more elongate over the condyle area; anticlinal walls of testa cells vertical so that the lumina are not funnel shaped; raphe passing obliquely through the condyle between limbs of the embryo cavity; limbs of embryo cavity circular in cross section, one slightly longer than the other; embryo cavity cast with a seam all along the margin representing to the plane of dehiscence.

Specimens.—Holotype: UF 6501, seed with intact seed coat. Paratypes: UF 9163, 9165, 9449, 9450, 9529–9542, 9543 (14 specimens), internal molds of seed coat.

Discussion.—*Cleyera grotei* is represented by numerous embryo cavity casts (i.e., internal molds of seed coat) from the Nut Beds showing the strongly curved embryo cavity (e.g., Pl. 42, figs. 3, 4). The holotype is a rare specimen with part of the reticulate seed coat adhering (Pl. 42, figs. 1, 2, 5). Embryo cavity casts of this species closely match those from the British Tertiary that were formerly ascribed to the fossil genus *Myrtospermum* Chandler. Although Chandler (1957) originally suggested that the seeds were myrtaceous, she subsequently recognized their affinities within the Theaceae (Chandler, 1960, 1961a), and later (Chandler, 1963b, p. 109) placed *M. variabile* (the type species of *Myrtospermum*) in synonymy with *Cleyera* (?) *stigmosa* (Ludwig) Chandler. She then transferred the other species formerly assigned to *Myrtospermum* to "*Cleyera*?" (Chandler, 1964, p. 40).

In shape and reticulate surface sculpture of the seed, the Nut Beds species resembles seeds of extant *Cleyera* and *Eurya* of the theaceous subfamily Ternstroemoideae. Friis (1985) studied these and related extant genera in reviewing fossil seeds of Theaceae from the Miocene of Europe. Seeds of *Cleyera* tend to be more strongly campylotropous and usually larger than those of the other genera. Friis (1985) also observed an important difference in the anticlinal walls of the testa cells that form the reticulate surface of the seed. In *Eurya*, the anticlinal walls decrease in thickness outward, so that the cell lumina are funnel-shaped, whereas in *Cleyera*, the same walls are uniformly thick so that the lumina are not funnel shaped (Friis, 1985). By this criterion, and on the basis of size and curvature, the Nut Beds seeds conform to *Cleyera*.

Cleyera is a genus of about 17 species with a disjunct distribution between southeast Asia (Himalayas to Japan) and tropical America (Mexico to Panama and West Indies). This genus has an excellent fossil seed record extending from the Eocene to the Late Tertiary of Europe (Mai, 1971).

Family ULMACEAE Mirbel.

The Ulmaceae, or elm family, includes 15 extant genera of trees and shrubs distributed in both the northern and southern hemispheres. Two subfamilies are recognized on the basis of differences in fruit, foliage and pollen characters (summarized in Manchester, 1989c): the Ulmoideae and the Celtidoideae. Although evidence has accumulated for the recognition of Celtidoideae as a separate family (Grudzinskaya, 1967; Chernik, 1980; Takaso and Tobe, 1990), I have retained the traditional treatment here. The Ulmaceae have an excellent fossil record that includes both extant and extinct genera (Manchester, 1989a, c). The Nut Beds flora includes at least three representatives of the Celtidoideae (*Aphananthe*, *Celtis*, *Trema*) and one of the Ulmoideae (*Cedrelospermum*). *Ulmus* is known from other localities of the Clarno Formation (West Branch Creek, White Cliffs, Sheep Rock Creek) on the basis of fruits and foliage (Manchester, 1989c) but has not been observed in the Nut Beds assemblage.

Subfamily CELTIDOIDEAE

Genus APHANANTHE Planchon

Aphananthe maii sp. nov.
Plate 42, figures 6–15

Aphananthe sp. Manchester, 1989c, p. 237, fig. 12.7, I-O.

Etymology.—This species is named for Dieter H. Mai, recognizing the importance of his contributions to paleocarpology.

Description.—Endocarp subglobose, unilocular, single-seeded, pyriform in cross section, elliptical to nearly circular in face view; asymmetrical, length 6.5–9.0, avg. 7.8 mm (SD=1.05, n=5), width 5.0–6.7, avg. 6.2 mm (SD=0.75, n=7), thickness 3.4–5.1, avg. 4.3 mm (SD=0.73, n=7), base rounded, apex rounded to acute, surface smooth to papillate; placental plug at the apex elliptical, oblique; endocarp with a prominent longitudinal crest deflected in course as it passes over the apex; endocarp wall 350–500 μm thick, consisting of a thin papillate locule lining of more or less isodiametric cells, a thick uniseriate layer of anticlinally oriented columnar cells 230–340 μm high, 17–28 μm wide, these cells thick-walled, with lumina closed except near the locule; conspicuous pits radiate from the lumina of these cells toward the locule (sometimes with crystal-bearing idioblasts in this layer); outside is a layer of translucent more-or-less rectangular cells that form papillae at the surface, 80–150 μm high, 130–180 μm wide. Locule cast smooth, similar in shape to the endocarp, but with sharper longitudinal crest. Seed with large embryo with a prominent coiled cotyledon.

Specimens.—Holotype: USNM 355693. Paratypes: UF 6518, 6519, 8808, 9328–9330, USNM 422384, 424629, 424718.

Discussion.—*Aphananthe maii* is represented by permineralized endocarps and locule casts that have been studied both by SEM of fractured surfaces (Pl. 42, figs. 11, 12) and light microscopy of serial sections (Pl. 42, figs. 13–15). The endocarps are virtually identical, anatomically as well as in size and morphology, to those of extant *Aphananthe*. Shared characters include the asymmetrical longitudinal keel, the endocarp wall with its thick uniseriate layer of anticlinally elongate sclereids (Pl. 42, figs. 14, 15), an outer silica layer forming a papillate surface (Pl. 42, figs. 6, 7), and a prominently coiled embryo (Pl. 42, fig. 13).

Aphananthe includes deciduous to semi-deciduous shrubs and trees distributed today from India to China, Korea, Japan, Indochina, Thailand, Malesia, the Philippines, Java, Madagascar, eastern Australia, the Solomon Islands, and Mexico. The Mexican species has sometimes been placed in a separate genus, *Mirandaceltis* A.J. Sharp, but its endocarp is virtually identical to that of the other species. This fossil species was illustrated but not named in a broader treatment of the Ulmaceae (Manchester, 1989c). Although this is the only known fossil occurrence of *Aphananthe* in North America, the genus is well-documented by endocarps from the Oligocene of western Siberia (Dorofeev, 1982).

Genus CELTIS L.

Celtis burnhamae sp. nov.
Plate 42, figures 16–25

Celtis sp. Manchester, 1989c, p. 240, fig. 12.8 A-C.

Etymology.—This species is named for Robyn J. Burnham, recognizing her contributions to the fossil history of Ulmaceae.

Description.—Endocarp subglobose, bilaterally symmetrical, unilocular, single-seeded, base rounded, apex rounded with a wedge-shaped tip, length 4.2–5.7, avg. 4.8 mm (SD=0.38, n=16), width in plane of symmetry 3.6–5.0, avg. 4.3 mm (SD=0.34, n=17), width at right angle to plane of symmetry 3.5–4.7, avg. 4.0 mm (SD=0.35, n=17); surface reticulate, with a pair of strong primary longitudinal ribs forming a keel in the plane of symmetry and usually a second pair of longitudinal ribs in the plane at right angles; secondary rib well-developed basally, weakening apically; a network of fine, vein-like ridges interspersed between the primary and secondary ribs, delimiting areoles 0.6–0.8 mm in diameter; apical prominence pierced by a small median funicular canal; pericarp 350–400 μm thick, consisting of three main layers: 1) innermost layer uniseriate consisting of large cuboidal, relatively thick-walled cells 50–70 μm in diameter, occasionally with rhomboidal crystals, overlain by 2) a thin uniseriate layer of interlocking digitate cells best seen in peridermal section; combined thickness of these two layers, i.e., the endocarp, ca. 100 μm, and 3) the outer layer, ca. 250–300 μm thick, composed of clear silica with poorly preserved, apparently isodiametric cells, ca. 20 μm in diameter. Locule cast taking form of the seed with large curved embryo, having the same plane of bisymmetry as the external fruit morphology, radicle projecting within the apical prominence of the endocarp; chalaza circular, on the opposite side of the locule cast from the radicle.

Specimens.—Holotype: UF 9600. Paratypes: UF 6520–6527, 8619–8640, 9579–9581, USNM 355466, 424644, 435050–435052, complete endocarps; USNM 355429, 422733, locule casts.

Discussion.—*Celtis burnhamae* endocarps and locule casts are especially abundant in the Nut Beds at the top of Face 3, although they are not known from other Clarno localities. Some specimens clearly show the external endocarp morphology with the characteristic pattern of ridges (Pl. 42, fig. 16–19); however, it is more common to find specimens that have broken along the layer of mechanical tissue giving a smooth, shiny appearance so that affinities to *Celtis* are not immediately obvious. The layer of interlocking digitate cells is seen in a few specimens that have broken peridermally at the appropriate level, seen with reflected light microscopy (Pl. 42, fig. 25). Locule casts show the seed morphology with the circular chalaza at one end (Pl. 42, fig. 20), and the tip of the radicle at the other (Pl. 42, fig. 21).

Although *Celtis* has a rich fossil record based upon fossil endocarps from the Tertiary of North America and Europe (Manchester, 1989c), the anatomical structure of these fossils in relation to the modern genus has not been considered. Sections of some of the Clarno specimens (Pl. 42, figs. 22–25) reveal anatomy that clearly conforms to that of the extant genus, which has been illustrated by Chernik (1980). These endocarps are larger, but morphologically similar to those of *C. edwardsii* Chandler from the late Eocene of England (Chandler, 1963a). A clear basis for distinguishing among the various extant species and among different fossil species based upon endocarp morphology has not been established. It is noteworthy, however, that *C. burnhamae* the uniseriate layer of cuboidal cells lining the locule is three to five times thicker than the corresponding layer in extant species that I have studied (*C. laevigata* Willd., *C. occidentalis* L., *C. pallida* Torr., *C. sinensis* Persoon).

Celtis is a genus of trees and shrubs that is wide-ranging in its present distribution, occurring in temperate and tropical regions of both the northern and southern hemispheres.

Celtis sp.

Plate 43, figures 1–5

Description.—Endocarp subglobose, bilaterally symmetrical, with a keel in the plane of symmetry, unilocular, single-seeded, base rounded, apex pointed; length 3.7–4.7, avg. 4.3 mm (SD=0.30, n=20), width in plane of symmetry 3.0–4.1, avg. 3.7 mm (SD=0.33, n=20), width at right angle to plane of symmetry 2.5–3.3, avg. 3.0 mm (SD=0.21, n=20); apical prominence pierced by a small median funicular canal, surface verrucate but without ridges, except for the longitudinal keel. Locule cast taking form of the seed, with a large curved embryo, radicle protruding within the apex of the endocarp; pericarp ca 200 μm thick with an inner layer of anticlinally elongate columnar cells 100–150 μm high, 50–90 μm wide; surrounded in some specimens by a translucent silica layer ca. 50 μm thick.

Specimens.—UF 8640–8658, 8659–8671, 9771–9775.

Discussion.—Endocarps of this species are common in the Nut Beds, represented by permineralized fruits and locule casts. The endocarps are similar in size and external morphology to those of *Celtis burnhamae*, but do not have a secondary ridge at right angles to the plane of bisymmetry, and have a verrucate (Pl. 43, figs. 1, 2) rather than reticulate (Pl. 42, fig. 17) surface. The fruits are somewhat compressed in the plane of symmetry (elliptical in cross section) rather than globose (circular in cross section) as in *C. burnhamae*. The curved embryo is apparent in specimens where part of the endocarp has flaked away revealing the curved locule cast (Pl. 43, fig. 3). When sectioned transversely, the partition between the radicle and the rest of the embryo is seen as a thin line bisecting the circle of the locule (Pl. 43, figs. 4, 5). The wall of these fruits is thin relative to that of *Celtis burnhamae* and extant species that I've examined, but the uniseriate columnar layer of the endocarp compares favorably between these taxa.

Among extant genera of Celtoideae, this species is most similar to *Celtis*. Because of the thin wall and lack of reticulate sculpture, it is possible that this species belongs in an extinct genus of the subfamily, but a more thorough morphological and anatomical investigation of extant *Celtis* fruits is needed before an informed decision can be reached.

Genus **TREMA** Loureiro

Trema nucilecta sp. nov.

Plate 43, figures 6–15

Etymology.—*Nucis* (L = nut) + *lectus* (L = bed), referring to the Nut Beds locality.

Description.—Endocarp subglobose, rounded-triangular in face view, bilaterally symmetrical, with a keel in the plane of symmetry, unilocular, single-seeded, length 2.0–3.0, avg. 2.5 mm (SD=0.21, n=16), width in plane of symmetry 1.9–2.6, avg. 2.3 mm (SD=0.26, n=15), width at right angles to plane of symmetry 1.8–2.4, avg. 2.1 mm (SD=0.18, n=15), base rounded, apex pointed with a circular scar at the tip; surface smooth; wall composed of uniseriate layer of anticlinally oriented columnar cells 100–120 μm high and 28–60 μm wide, these cells with fenestrate walls having numerous orbicular pits; apical funicle bulge composed of small isodiametric cells ca. 8 μm in diameter; poorly preserved silica layer 50 μm thick surrounding the mechanical layer. Locule cast shaped like the endocarp, but with a sharper keel, embryo large, coiled with a prominent curved radicle; seed coat ca. 10 μm thick, composed of isodiametric cells.

Specimens.—Holotype: UF 9781. Paratypes: UCMP 10732–10737, UF 6791–6799, 9585, 9776–9780, 9782–9788, 9791, USNM 355097 (12 specimens), 424635, 424723.

Discussion.—*Trema nucilecta* is represented by permineralized endocarps (Pl. 43, figs. 6–10) and chalcedony locule casts (Pl. 43, figs. 11–13). The locule casts are curved, reflecting the embryo shape (Pl. 43, figs. 8, 13). The specimens are similar in overall shape of endocarp and locule cast to *Celtis* sp. (see above), but are readily distinguished by smaller size, smooth exterior, and thinner, endocarp wall composed of more elongate columnar cells. This species conforms very well in size, shape, wall anatomy and embryo curvature to extant *Trema*. One difference noted between the fossil species and the extant species examined was the lack in the fossil of a secondary ridge running at right angles to the plane of symmetry.

Subfamily **ULMOIDEAE**

Genus **CEDRELOSPERMUM** Saporta

Cedrelospermum lineatum

(Lesquereux) Manchester

Plate 43, figures 16–18

Cedrelospermum lineatum (Lesquereux) Manchester, 1987b, p. 124.
Banksites lineatus Lesquereux, 1883, p. 165, pl. 32, fig. 21. [more complete synoymy in Manchester 1987b].

Description.—Fruit a samara, consisting of a flattened elliptical endocarp adjoined by an elongate lateral wing; samara length 12.5–15.5, avg. 13.8 mm (SD=1.31, n=8); endocarp length 4.7–5.0, avg. 4.7 mm (SD=0.14, n=5), width 2.3–3.0, avg. 2.7 mm (SD=0.27, n=5); primary wing length 9.7–11.5 mm, width 4.5–

5.0 mm, oriented oblique to the long axis of the endocarp with 6–8 subparallel veins, including marginal veins that converge toward stigmatic area at the adaxial margin of the distal end of the wing; a small secondary wing 1.0–2.0 mm long, oriented nearly parallel to the long axis of the endocarp.

Specimens.—OMSI Pb565, 586, 764, 1108, 1109, 1128, 1322, 1323, 1502, 1636, UF 9285. (Lectotype: USNM 387567 from Florissant, Colorado [Lesquereux, 1883, pl. 32, fig. 21]).

Discussion.—*Cedrelospermum lineatum* samaras are preserved in the Nut Beds as impressions in siltstone. They were recovered only from a 1 meter-wide area of the leaf-bearing horizon at the base of Face 3 in a concentration of winged fruits that also included *Deviacer*. *Cedrelospermum* is known from nearly all Clarno paleobotanical localities. For comparative purposes, the dimensions in the above description are deliberately limited to specimens from the Nut Beds. In the large size of endocarp and overall fruit length, this material conforms to *C. lineatum*, a species based upon specimens from Florissant, Colorado (Manchester, 1989a). Fruits from other localities of the Clarno Formation (e.g., West Branch Creek, Gosner Road, Teater Road) are smaller and appear to belong to another species, *C. nervosum*, which is based upon material from the Green River Formation of Colorado, Utah and Wyoming (Manchester, 1989a).

Cedrelospermum Saporta is an extinct genus of Ulmaceae known from the late Eocene to late Miocene of Europe and the middle Eocene to Oligocene of western North America (Manchester, 1987b, 1989a, c). Recently, the genus has also been confirmed from Neogene strata near Tepexi de Rodriguez, Puebla, Mexico (Magallón-Puebla and Cevallos-Ferriz, 1992), indicating a southern refugial population. *Cedrelospermum nervosum* and *C. lineatum* fruits have been found attached to fossil twigs bearing narrow *Zelkova*-like leaves in the Eocene of Utah and Colorado (Manchester, 1989a). Characters of the fruits and foliage and of attached staminate flowers and pollen establish clear affinities with the Ulmoideae (Manchester, 1989a, c).

Family **VITACEAE** Jussieu

The Vitaceae (grape family) include eleven extant genera and about 800 species of lianas distributed in tropical to warm temperate regions. Seeds of this family are well represented in the Tertiary of the northern hemisphere as reviewed by Kirchheimer (1938), Tiffney and Barghoorn (1976) and Cevallos-Ferriz and Stockey (1990).

The Vitaceae are diverse in the Nut Beds, representing at least four genera: *Ampelocissus* (2 spp.), *Ampelopsis*, *Parthenocissus* (2 spp.) and *Vitis* (2 spp.).[4] For the descriptions that follow, I use the terminology recommended by Tiffney (1976), with the exception that the terms chalaza-base groove and chalaza-apex groove are reversed so that base refers to the hilar/micropylar end of the seed and apex to the opposite, rounded end. Extant genera overlap to some extent in seed morphology, and the evaluation of fossil remains is hampered by the lack of a thorough systematic work on seed morphology indicating characters that are diagnostic at the generic level. Some morphological patterns appear to be confined to a single genus, while others occur in more than one modern genus.

Genus **AMPELOCISSUS** Planchon

Ampelocissus auriforma sp. nov.
Plate 44, figures 16–18, 22

Parthenocissus? sp., Scott, 1954, p. 82 , pl. 16, fig. 15.

Etymology.—*Aurus* (L = ear) + *forma* (L = shape) referring to the shape of the enlarged ventral infolds.

Description.—Seed cordiform in face view, epsilon-shaped in cross section, bilaterally symmetrical, base pointed, apex emarginate. Internal mold of seed coat length 3.5–7.1, avg. 5.4 mm (SD=1.04, n=28), width 3.2–6.2, avg. 4.9 mm (SD=0.93, n=28), thickness 2.0–3.8, avg. 2.9 mm (SD=0.49, n=26); dorsal surface convex, with a central elliptical to circular depression representing the chalaza, and a pronounced median groove passing from the base to the apex and over to the apex of the ventral surface; faint ruminations radiating from the chalaza; ventral infolds represented by a pair of large, smooth, elliptical, cup-like cavities separated by a thin median longitudinal raphal septum; lateral limbs of the seed 0.5–0.7 mm thick; seed coat ca 125 μm thick, with a uniseriate layer of anticlinally oriented columnar cells.

Specimens.—Holotype: UF 6572. Paratypes: HU 59960, UCMP 10568–10578, UF 6543, 6571, 9524, 9620–9624, UM 29935, 39564 (5 specimens), USNM 355082, 355083 (10 specimens), 434987–434997.

Discussion.—This species is relatively common in the Nut Beds. Specimens are usually preserved as silica molds of the inside of the seed coat (Pl. 44, figs. 16, 17. These internal seed coat molds are commonly recovered within sedimentary molds of the outer seed surface. Such molds of the ventral seed surface have a distinctive bilobed appearence due to infilling of the pair of ventral infolds (Pl. 44, fig. 18). Scott (1954) figured and described specimens of this species as *Parthenocissus*? sp. and interpreted the specimens to represent detached dorsal sides of seeds similar to *P. angustisulcata*. However, transverse sections show that

---

[4] For new information on wood, see note added in proof, p. 200.

the seed coat is intact on both the dorsal and ventral sides and that the concave aspect of the ventral surface is an original feature (Pl. 44, fig. 22).

The large cup-like ventral infolds of *Ampelocissus auriforma* distinguish it from all other Nut Beds Vitaceae and are useful in generic placement. Seeds with comparably large infolds have been observed in some of the extant species of *Ampelocissus*, for example: *A. martinii* Planch. from the Philippines, *A. imperialis* from Java and *A. costaricensis* Lundell from Costa Rica. Although reports of *Ampelocissus* from the North American fossil record are rare, the genus was probably widely distributed in the Eocene; a single specimen preserved as a bilobed mold similar to this species is known from the Middle Eocene Green River Formation of Utah (UF 8207, loc. 15755). Cevallos-Ferriz and Stockey (1990) reported another species based upon anatomically preserved seeds from the Middle Eocene Princeton chert of British Columbia. The Princeton chert species lacks the enlarged ventral infolds. *Ampelocissus* is a genus with about 95 extant species, of tropical distribution.

Ampelocissus scottii sp. nov.
Plate 44, figures 11–15

Etymology.—This species is named after Richard A. Scott.

Description.—Seed cordate, bilaterally symmetrical; length 5.9, 5.9, 6.0 mm, width 4.8, 5.4, 6.0 mm, thickness 2.7, 2.7, 2.8 mm; ventral infolds short, about ⅓ as long as the seed, nearly parallel, slightly divergent apically, becoming wider in the apical ⅓ of the length; chalaza circular, central; chalaza-apex groove broad, chalaza-base groove indistinct, dorsal surface convex, with a central elliptical to circular chalaza. Internal mold of seed coat length 4.9–5.1 mm, width 3.9–5.4 mm, thickness 2.2–3.5 mm; dorsal surface convex, with a central elliptical to circular depression representing the chalaza, and a pronounced median groove passing from the base to the apex and over to the apex of the ventral surface; faint ruminations radiating from the chalaza.

Specimens.—Holotype: USNM 424665, seed. Paratypes: UF 6545, USNM 355083, 355119, 434984, 435118, seeds; UF 6542, 6544, internal molds of seed coat.

Discussion.—*Ampelocissus scottii* resembles *A. auriforma* in shape, size and morphology of the apex, base and dorsal surface. However, instead of the large cup-like ventral infolds, this species has short narrow divergent infolds (Pl. 44, fig. 11). Lacking the distinctive character of large ventral infolds, which to my knowledge is confined to *Amplelocissus*, the assignment of this species to the genus is less secure. However, not all extant species of *Ampelocissus* have enlarged infolds. With its rugulate margins, broad chalaza-apex groove, and short divergent infolds, this fossil resembles the seeds of some extant species of *Ampelocissus*, such as *A. arachnoideus* (Haask.) Planch.

In general form, specimens of this species resemble those of *Ampelopsis rooseae* (Pl. 44, figs. 6–10), but they are much larger, more compressed dorsiventrally, and do not possess a chalaza-apex ridge.

Genus AMPELOPSIS Michaux

Ampelopsis rooseae sp. nov.
Plate 44, figures 6–10, 21

Tetrastigma, Bones, 1979, pl. 4, fig. 10.

Etymology.—This species is named for Carrie L. Roose, acknowledging her technical assistance in this investigation.

Description.—Seed subglobose, bilaterally symmetrical, rounded-triangular in dorsal and ventral views with smooth contours, slightly pointed at the base (hilum) in complete seeds, apex emarginate to broadly rounded, length of seed casts with intact seed coat 3.0–4.3, avg. 3.6 mm (SD=0.36, n=8), width 2.8–3.7, avg. 3.1 mm (SD=0.31, n=8), thickness 2.0–2.7, avg. 2.3 mm (SD=0.23, n=8); chalaza typically spatulate, occasionally round, located in the central one-half to apical one-third of the seed on the dorsal surface; dorsal surface smooth or slightly ruminate; chalaza-base groove present, narrow; chalaza-apex groove absent on the seed surface, although sometimes present on internal molds of the seed coat; chalaza and apex typically joined by a ridge that passes over the apex and joins with the raphe ridge; ventral infolds long and straight, diverging apically, becoming wider in upper third of their length, extending from a position well above the seed base and terminating approximately ¾ of the length of seed toward the apex; groove corresponding to raphe preserved on the raphe ridge in complete seed casts; seed coat 130–150 μm thick. Internal mold of seed coat sharply pointed basally, length 2.5–4.5, avg. 3.3 mm (SD=0.41, n=36), width 2.3–4.1, avg. 3.0 mm (SD=0.37, n=36), thickness 1.5–2.8, avg. 2.1 mm (SD=0.30, n=36).

Specimens.—Holotype: UF 6536, seed cast. Paratypes: UCMP 10596–10597, UF 6537, 6538, 9575, 9659, 9660, 9661, USNM 312768, 312769 (Bones, 1979, pl. 4, fig. 10), 355122 (2 specimens), seed casts; UCMP 10598–10606, UF 6538, 9662–9691, USNM 355090 (20 specimens), 355093 (106 specimens), internal molds of seed coat.

Discussion.—This species is similar in size to the seeds of *Vitis tiffneyi* but it is distinguished by its ventral infolds, which are longer and divergent, rather than parallel, and by the well-developed raphe ridge that typically passes over the apex to join with the chalaza.

Most specimens are globular, suggesting one-seed per berry, but in some of the seeds the ventral surface has flattened facets suggesting more than one seed per berry.

Seeds with short divergent ventral infolds occur in some of the extant species of *Ampelopsis* and *Vitis*. Whereas *Vitis* seeds generally have a chalaza-apex groove, those of *Ampelopsis* lack such a groove and typically have a ridge in the same position, as does this fossil. *A. rooseae* bears a close resemblance to *Ampelopsis monasteriensis* Kirchheimer (= *A. rotundata* Reid et Chandler 1933 auct non Chandler 1926; Chandler 1961b) from the Eocene London Clay flora. A compression specimen that appears to be identical to this Nut Beds species is known from the Eocene Green River Formation near Watson, Utah (UF 8206, loc. 15755).

Genus **PARTHENOCISSUS** Planchon

Parthenocissus angustisulcata Scott
Plate 45, figures 6, 7

Parthenocissus angustisulcata Scott 1954, p. 81, pl. 16, fig. 14.
Vitaceae. Undetermined genus, Bones, 1979, pl. 4, figs. 11, 12.

Description.—Seed cast subglobose, obovate in face view, bilaterally symmetrical to asymmetrical, length 5.4–6.4, avg. 6.0 mm (SD=0.45, n=3), width 4.6–5.5, avg. 5.1 mm (SD=0.45, n=3), thickness 2.9–4.3, avg. 3.5 mm (SD=0.74, n=3), surface usually smooth, but undulating in some specimens, ventral infolds long, slightly curved, diverging apically, extending from the very base of the seed to the apical ⅙ of the seed, raphe ridge triangular, slightly raised above the seed body, chalaza circular to spatulate, centrally positioned, faint ruminations radiating from chalaza over the dorsal surface; chalaza-base groove and chalaza-apex groove well developed.

Specimens.—Holotype: UM 29934 (Scott, 1954, pl. 16, fig. 14). Hypotypes: UF 6544, 9737, 9738, 9880–9882, USNM 355128, 434986.

Discussion.—This species was described by Scott (1954) on the basis of a single specimen showing the ventral side only. More complete seeds now available also show the dorsal surface, with a pronounced chalaza-base groove (Pl. 45, fig. 7) and give a better understanding of the variability within the species, enabling the more complete description provided above. As Scott noted, important features of *Parthenocissus angustisulcata* include the deep apical notch marking the course of the raphe, and long, narrow, divergent ventral infolds (e.g., Pl. 45, fig. 6).

The long narrow, apically divergent ventral infolds and narrow raphe ridge were used to place this in *Parthenocissus*. Scott noted that it differs from the modern species and from *P. monasteriensis* (Reid et Chandler) Scott of the London Clay flora by its larger size. Whether this size difference and the pronounced apical cleft are admissable within *Parthenocissus* is open to further investigation.

Parthenocissus clarnensis sp. nov.
Plate 45, figures 1–5

Etymology.—The epithet refers to the Clarno Formation.

Description.—Seed subovoid, obovate in face view; cross section rounded in some, rounded-triangular in others, due to variable development of ventral facets, bilaterally symmetrical to asymmetrical; length 3.0–4.8, avg. 3.8 mm (SD=0.45, n=25), width 2.8–4.2, avg. 3.4 mm (SD=0.36, n=25), thickness 2.0–3.5, avg. 2.2 mm (SD=0.34, n=25); ventral infolds long, slightly curved, diverging apically, extending from the very base of the seed to the apical ⅙ of the seed, raphe ridge triangular slightly raised above the seed body, surface usually smooth, but undulating in some specimens, chalaza typically spatulate, occasionally round, positioned central or somewhat offset toward the apex, radiating undulations usually week, chalaza-base groove absent or faint, chalaza apex-groove present, weak (stronger in the globose specimens, weaker in the faceted ones); seed coat 200–300 μm thick, with a uniseriate layer of columnar cells 200 μm high and 12–16 μm thick and an outer layer 40 to 80 μm thick composed of isodiametric cells ca. 14–18 μm in diameter.

Specimens.—Holotype: UF 6539. Paratypes: UCMP 10584, 10595, UF 6540, 6541, 9583, 9693–9717, USNM 355085 (19 specimens), 355087 (7 specimens), 355088 (12 specimens), 355089 (12 specimens), 355091 (12 specimens) 355100 (28 specimens), 355134 (8 specimens).

Discussion.—*Parthenocissus clarnensis* is characterized by long, divergent ventral infolds, a lack of a chalaza-base groove and weak to well-developed chalaza-apex groove (Pl. 45, figs. 1–4). Some of the specimens are relatively globose and probably were borne one per fruit. Others have one or two flattened faces on the ventral side suggesting that they were borne two or more per fruit. It is much more common than *P. angustisulcata*, which has larger seeds with more pronounced chalaza-base and chalaza-apex grooves.

This species resembles *Parthenocissus monasteriensis* (Reid et Chandler) Scott from the London Clay flora and is similar to extant *P. vatascea* from northern Mexico and *Vitis amurensis* J.Y. Li from Siberia.

Genus **VITIS** L.

Vitis magnisperma Chandler
Plate 45, figures 8–13

Vitis magnisperma Chandler 1961b, p. 247, pl. 24, figs. 29, 30.
Vitis, Bones, 1979, pl. 4, fig. 9.

Description.—Internal mold of seed coat more or less elliptical in face view, truncate or emarginate apically with a slight to well-developed chalaza-apex groove, chalaza-base groove faint or absent; length 7.0–10.3, avg. 8.9 mm (SD=1.09, n=6), width 5.5–6.9, avg. 6.2 mm (SD=0.57, n=6), thickness 2.8–3.0, avg. 2.9 mm (SD=0.10, n=4); ventral infolds long, somewhat divergent apically, straight to curved, extending from the extreme base to the apical ⅙ of seed; chalaza circular to cordate, centrally positioned; faint ruminations radiate around the chalaza and over the dorsal surface; chalaza-apex groove well developed, chalaza-base groove faint or absent.

Specimens.—UCMP 10607, UF 9735, 9879, USNM 312761 (Bones, 1979, pl. 4, fig. 9, right), 355095, 355098, 355127 (Bones 1979, pl. 4, fig. 9, left), 355130, 434985.

Discussion.—This species includes the largest vitaceous seeds known from the Nut Beds, some a full centimeter in length. Only internal molds of the seed coat are represented, so the full size of the seed was somewhat larger. With its elongate ventral infolds, shallow chalaza-apex groove and ruminations emanating from the chalaza, this species does not differ in any essential characters from those in the London Clay described as *Vitis magnisperma* Chandler (Chandler, 1961b). These seeds are larger than those typical of extant *Vitis* species, and the species might represent another genus. However Chandler's assignment is retained pending further comparative work with extant Vitaceae.

Vitis tiffneyi sp. nov.

Plate 44, figures 1–5, 19, 20

Etymology.—This species is named for Bruce H. Tiffney in recognition of his contributions to paleobotany and the study of fossil vitaceous seeds.

Description.—Seed subglobose, bilaterally symmetrical, with smooth contours, pointed at the base (hilum), apex slightly emarginate; length of complete seed, with seed coat intact 3.7–4.0, avg. 3.9 mm (SD=0.14, n=5), width 3.2—3.5, avg. 3.4 mm (SD=0.13, n=5), thickness 2.3–2.7, avg. 2.5 mm (SD=0.14, n=5); chalaza circular to elliptical, positioned centrally on the dorsal surface, sometimes surrounded by weak radiating undulations; chalaza-base groove moderate, chalaza-apex groove pronounced, extending over the seed apex and merging with the raphal ridge of the ventral side; paired ventral infolds straight, short, approximately half the length of the seed, oriented nearly parallel to one another; with a fine groove at surface of raphe ridge; raphe ridge widening only slightly, if at all, toward the apex; seed coat 90–100 μm thick, with a uniseriate layer of columnar cells ca. 90 μm high and 15–20 μm wide. Internal mold of seed coat morphologically similar to the seed surface but with sharp base, emarginate apex, length 2.8–3.8, avg. 3.3 mm (SD=0.24, n=40), width 2.4–3.3, avg. 2.9 mm (SD=0.19, n=40), thickness 1.3–to 2.8, avg. 2.0 mm (SD=0.27, n=40).

Specimens.—Holotype: UF 6534, seed cast. Paratypes: UF 9573, 9625–9628, complete seed casts; HU 60070 (Tiffney and Barghoorn, 1976, pl. II, J), UCMP 10579–10583, UF 6563, 6535, 9572, 9629–9658, USNM 355094 (26 specimens), 355102 (20 specimens), internal molds of seed coat.

Discussion.—The distinctive features of this seed type are the parallel, relatively short ventral infolds, typically circular chalaza, bisymmetry and pronounced chalaza-apex groove. The species is abundant in the Nut Beds, represented both by complete seed casts with the seed coat intact (Pl. 44, fig. 1, 2) and by molds of the inside of the seed coat (Pl. 44, figs. 4, 5). Some of the complete seed casts have a portion of the seed coat fractured away, showing a relatively thin seed coat, and revealing the internal mold of the seed coat (Pl. 44, fig. 3). The internal molds, most abundant at the locality, are distinguished by the more sharply pointed hilar projection and by the outline of broken testa surrounding each of the ventral infolds. In general size and outline, these specimens can be confused with those of *Ampelopsis rooseae*, however, the latter are distinguished by having divergent (Pl. 44, figs. 6, 8, 10), rather than parallel (Pl. 44, figs. 1, 4) ventral infolds and a thicker seed coat (cf. Pl. 44, figs. 3, 7, 19, 21).

This species is similar in shape and size to *V. subglobosa* Reid et Chandler from the London Clay (Reid and Chandler, 1933; Chandler, 1961b). Tiffney and Barghoorn (1976) examined this Clarno species and noted that the short, wide ventral infolds indicate similarity to seeds of extant *Ampelopsis* and to many Paleogene species, including *Vitis subglobosa* Reid et Chandler, *Ampelopsis crenulata*, *A. monasteriensis* (*A. rotundata* emend. Chandler 1960), *Vitis platyformis*, *V. rectisulcata*, *Palaeovitis paradoxa* Reid et Chandler, *V. obovoidea* Chandler. Affinities to *Ampelopsis* probably can be ruled out by the absence of a well-developed chalaza-apex ridge. Based on their examination of this species from the Nut Beds, Tiffney and Barghoorn (1976, p. 185) observed that the "The combination of distinctive infolds with other *Vitis* characters leads one to suspect that they represent either an unrecognized modern form or an extinct lineage in the genus *Vitis*."

INCERTAE SEDAE

Genus **ANKISTROSPERMA** gen. nov.

Etymology.—*Ankistron* (Gr = fish hook) + *sperma* (Gr = seed), referring to the J-shape of the seed.

Type species.—*Ankistrosperma spitzerae* sp. nov.

Ankistrosperma spitzerae sp. nov.
Plate 46, figures 11–13

Etymology.—The epithet recognizes contributions of Josephine Spitzer to this project.

Description.—Cast J-shaped, often bilaterally symmetrical, circular in cross section, pointed at short end, blunt or truncate at long end; length 2.0–2.9 mm, width across plane of symmetry 0.7–0.9 mm, constricted in the apical region into a cylindrical neck 0.3–0.5 mm long, surface smooth.

Specimens.—Holotype: UF 9806. Paratypes: UF 9807–9814, 9815 (10 specimens), USNM 355568 (22 specimens), 355571.

Discussion.—This species is based upon distinctive J-shaped casts that appear to represent seeds with a curved embryo and a constricted, neck-like hilar area (Pl. 46, figs. 11–13). The short, pointed end might represent the micropyle. Affinities with respect to modern families are unknown.

Genus **ANONYMOCARPA** gen. nov.

Etymology.—*Anonymos* (Gr = nameless, unknown) + *karpos* (Gr = fruit), referring to the uncertain familial affinities of this fruit.

Type species.—*Anonymocarpa ovoidea* sp. nov.

Anonymocarpa ovoidea sp. nov.
Plate 45, figures 14–17

Etymology.—*Ovatus* (L = egg-shaped) + *oid* (Gr = like, resembling), referring to the endocarp shape.

Description.—Fruit ellipsoidal, circular in cross section, rounded apically and basally, unilocular, single-seeded; length 29 mm, equatorial diameter 22 mm, pericarp consisting of three layers: 1) inner layer 120–140 μm thick, uniseriate, composed of anticlinally elongate cells 120–140 μm high, 20–30 μm wide, 2) middle layer 400 μm thick composed of longitudinally oriented fibers, 50–100 μm wide, 3) outer layer about 400 μm thick composed of narrow, horizontal, periclinally oriented fibers, this outer layer with prominent longitudinal vascular bundles up to 200 μm in diameter.

Specimen.—Holotype: USNM 355614.

Discussion.—This species is known from one fruit that has been sectioned transversely to show the single locule and wall structure. Although the fruit is anatomically distinctive, its systematic affinities remain obscure.

Genus **ASCOSPHAERA** gen. nov.

Etymology.—*Asco* (Gr = bag, bladder) + *sphaero* (Gr = ball), referring to the sack-like form of the fruit and spheroidal form of the seed.

Type species.—*Ascosphaera eocenis* sp. nov.

Ascosphaera eocenis sp. nov.
Plate 46, figures 6–10

Etymology.—The epithet refers to the Eocene age of the Nut Beds deposit where this species occurs.

Description.—Fruit bulb-shaped, radially symmetrical, unilocular, single-seeded, circular in cross section, length 3.1–4.4 mm, width 2.0–3.0 mm, surface rough; fruit wall 0.4–0.6 mm thick with an outer layer of polygonal cells 100–200 μm in diameter. Locule cast spheroidal, length 2.0–2.1 mm, equatorial diameter 1.7–1.8 mm, smooth, with a circular truncation at the base, and a slight rise at the apex, sometimes with a faint longitudinal groove (raphe?).

Specimens.—Holotype: UF 6318. Paratypes: UF 6319, 6320, 9789, 9790, 9873, fruits; UF 6343, 6415, 9770, USNM 424753, 424759, 424789, locule casts.

Discussion.—This species is represented by silicified fruits shaped like light bulbs (Pl. 46, figs. 6, 7) and globose locule casts (Pl. 46, figs. 8, 9). A fractured fruit with the locule cast partially exposed (Pl. 46, fig. 7) helps to establish the link between the complete fruits and isolated locule cast specimens.

Genus **AXINOSPERMA** gen. nov.

Etymology.—*Axine* (Gr = Ax, wedge) + *spermum* (Gr = seed).

Type species.—*Axinospermum agnostum* sp. nov.

Axinosperma agnostum sp. nov.
Plate 46, figures 1–5.

Etymology.—*Agnostos* (Gr = unknown, unknowing), alluding to the unknown affinities of this taxon.

Description.—Seed bilaterally symmetrical, more or less elliptical with rounded base and apex as seen in lateral view; laterally compressed with a median keel developed apically and ventrally in the plane of symmetry, length 1.9–2.2 mm, width in the plane of symmetry 1.2–1.6 mm, thickness across the plane of symmetry 0.7–1.0 mm, surface smooth, hilum subapical and ventral in the plane of symmetry; embryo cavity elongate, curved ventrally, circular in cross section.

Specimens.—Holotype: UF 6290. Paratypes: UF 9799, 9800, 9816–9829, USNM 424711–424713, 424716, 424736.

Discussion.—These small seeds are preserved as silica casts. The laterally flattened shape and the keel along the apical and dorsal margins in the plane of symmetry are distinctive features. Sometimes the apical crest is broken away, revealing a lobe of the embryo cavity (Pl. 46, figs. 3, 4). A transversely sectioned seed (Pl. 46, fig. 5) reveals the elliptical cross section of the embryo cavity.

Genus **BONESIA** gen. nov.

Etymology.—Named in memory of Thomas J. Bones, the collector.

Type species.—*Bonesia spatulata* sp. nov.

Bonesia spatulata sp. nov.
Plate 47, figures 1–10

Etymology.—*Spatula* (L = diminutive of *spatha*, a broad blade, paddle for stirring) referring to the spatulate shape of the locule casts.

Description.—Fruit unilocular, single-seeded, wide-elliptical in face view, dorsiventrally flattened, elliptical or lenticular in cross section; quadrilaterally symmetrical about the longitudinal axis, base and lateral margins rounded, apex mucronate, surface smooth with a low-rounded, median longitudinal ridge extending from the base to the apex on both dorsal and ventral sides; pericarp 0.5 mm thick, composed of an inner layer of radial files of isodiametric sclereids 50–63 μm in diameter and a uniseriate outer layer of anticlinally oriented columnar sclerenchymatous cells 83 μm high, 12–15 μm wide. Locule cast smooth, similar in shape to endocarp, with a circular basal depression approximately 1 mm in diameter, locule cast length 4.3–6.2, avg. 5.0 mm (SD=0.5, n=14), width 3.9–5.2, avg. 4.5 mm (SD=0.39, n=14), thickness 1.4–2.4, avg. 1.9 mm (SD=0.31, n=14); seed with a thin shriveled seed coat and large embryo with a pair of planar cotyledons.

Specimens.—Holotype: USNM 424642. Paratypes: UCMP 10728, 10729, UF 6355, 8583, 8584, 9398–9404, 9472, USNM 354057 (3 specimens), 424643, 435088.

Discussion.—*Bonesia spatulata* fruits usually are preserved as white translucent chalcedony locule casts that are readily identified by their dorsiventral flattening, slightly raised median dorsal and ventral ridges, slight apical beak (Pl. 47, figs. 1–4) and prominent basal circular scar (Pl. 47, figs. 4–6). Occasionally part of the fruit wall is preserved and may be sectioned to reveal a relatively thick endocarp with an outer uniseriate columnar layer (Pl. 47, figs. 8, 10). Sections through the locule casts reveal a single seed within the locule, with a pair of large, planar cotyledons (Pl. 47, figs. 8, 9).

Genus **COMMINICARPA** gen. nov.

Etymology.—*Comminus* (L = near, at close quarters) + *karpos* (Gr = fruit), referring to the close spacing of fruits within the infructescence.

Type species.—*Comminicarpa friisae* sp. nov.

Comminicarpa friisae sp. nov.
Plate 48, figures 1–7

Etymology.—The epithet recognizes the contributions of Else Marie Friis to paleobotany.

Description.—Infructescence spike-like, at least 16 mm long, and 10 mm in diameter consisting of numerous achenes closely packed together on an elongate axis, perianth not evident. Fruits apparently grouped in threes, more or less obovate, laterally faceted and angular-subrounded in cross section through crowding effect of neighboring fruits, cuneate in longitudinal section, narrowed basally, apex truncate-rounded with central protruding style; fruit length 2.5–2.8 mm, width 0.85–1.1 mm; pericarp 80–100 μm thick, composed mostly of isodiametric cells about 10–15 μm in diameter, but with an intermittent middle uniseriate layer of large rectangular to subrounded cells 30–50 μm in diameter that appear to be idioblasts. Fruits unilocular with a single seed pendulous from the apex. Seed coat consisting of a thin layer of narrow (5 μm) axially elongate cells.

Specimens.—Holotype: USNM 355697. Paratypes: UF 9349, 9582, 9874–9878.

Discussion.—This species is represented by one infructescence (Pl. 48, figs. 1–3, 5) and several specimens with isolated achenes in close proximity scattered in small pieces of sediment. The fruits are achenes, each with a prominent central style. The seed coat is well preserved and appears to have been well cutinized.

Genus **CUNEISEMEN** gen. nov.

Etymology.—*Cuneus* (L = wedge) + *semen* (L = seed).

Type species.—*Cuneisemen truncatum* sp. nov.

Cuneisemen truncatum sp. nov.
Plate 47, figures 11–16

Etymology.—*Truncus* (L = cut off), referring to the apical facet.

Description.—Seed/pyrene elongate, typically bisymmetrical, shaped like a lemon segment, with a rounded dorsal face and a pair of relatively flat ventral faces meeting at an angle of ca. 50–60°, giving a rounded-triangular cross section, truncate apically with a triangular facet, ca. 0.9–1.2 mm in diameter, bluntly pointed at the base; length 4.0–4.8, avg. 4.6 mm (SD=0.60, n=9), width 2.2–3.1, avg. 2.5 mm (SD=0.30, n=9), dorsiventral thickness 2.1–2.5, avg. 2.3 mm (SD=0.13, n=9), dorsal and ventral faces very finely striate longitudinally; outer coat thin, terminating apically in a rim around the truncation.

Specimens.—Holotype: UF 6392. Paratypes: UCMP 10687, UF 9362, 9364–9368, 9724.

Discussion.—This species is represented by wedge-shaped chalcedony casts that appear to represent pyrenes or seeds. The angular shape suggests that they may have been borne close together in the fruit. Of eight specimens, seven are bilaterally symmetrical, with the plane of symmetry bisecting the ventral angle (Pl.

47, figs. 11, 15) and one is asymmetrical (Pl. 47, fig. 16), possibly distorted through ontogeny. The outer covering (seed coat or exocarp?) forms a rim around, but does not cover, the apical truncation (Pl. 47, fig. 14), indicating that the truncation is probably the attachment scar. The familial affinities of this taxon remain undetermined.

Genus **DENTISEMEN** gen. nov.

Etymology.—*Dentis* (L = tooth) + *semen* (L = seed)
Type species.—*Dentisemen parvum* sp. nov.

Dentisemen parvum sp. nov.
Plate 46, figures 14–17

Etymology.—*Parvus* (L = little), referring to the small seed size.

Description.—Seed cast trigonal in outline with flat base and pointed apex, rounded dorsally, bilaterally symmetrical, with a median longitudinal infold or slit on the ventral surface in the plane of symmetry extending from the apex to a point about ⅓ of the distance from the base; length 2.5–2.7 mm, width 1.4–1.7, thickness 1.0–1.3 mm; surface micro-verrucate.

Specimens.—Holotype: UF 9766. Paratypes: UCMP 10738, UF 9767, USNM 355434, 355670.

Discussion.—These appear to be internal molds of seed coat. They are preserved in white chalcedony, without cellular detail. Although distinctive in the flat base, median ventral slit (Pl. 46, figs. 14, 16) and verrucate surface (Pl. 46, figs. 16, 17), the affinities among extant families remain unknown.

Genus **DUROCARPUS** gen. nov.

Etymology.—*Durus* (L = hard, tough, lasting) + *karpos* (Gr = fruit).
Type species.—*Durocarpus cordatus* sp. nov.

Durocarpus cordatus sp. nov.
Plate 48, figures 8–13

Etymology.—The epithet, *cordatus* (L = heart-shaped) refers to the seed outline.

Description.—Fruit wide obovate in face view, elliptical in cross section, quadrilaterally symmetrical with the two planes of symmetry intersecting at right angles in the vertical axis; in face view apex more or less flat, base wide-cuneiform; length 5.5 mm, width 6.0 mm, thickness 3.9 mm; bicarpellate and bilocular with one seed per locule; surface smooth and rounded; pericarp thick, 1.2 mm, septum 2 mm thick; locules obovate, 1.8 mm high, 0.8 mm wide, placentation ventral near the apex of locule, ovules pendulous; a central column of vascular strands passing medially from the base to the apex, tapering toward the apex; locule lining and endocarp composed of a four- to ten-seriate layer of thick-walled isodiametric cells 25–60 μm in diameter; mesocarp, forming the bulk of tissue between and surrounding the two endocarps, composed of thin-walled cells 42–75 μm in diameter, with islands of thick-walled cells similar to those of the endocarp, prominent branching vascular strands and lacunae filled with dark contents, exocarp not preserved.

Specimen.—Holotype: UF 6110.

Discussion.—*Durocarpus* is represented by a single specimen that is a distinctive bilocular, relatively thick-walled fruit. The specimen was sectioned longitudinally (Pl. 48, fig. 10), revealing the ventral, subapical placentation (Pl. 48, figs. 11, 12), then reassembled and sectioned transversely (Pl. 48, fig. 13). The fruit anatomy is well preserved. Extant families with similar characteristics include Anacardiaceae, Euphorbiaceae, Meliaceae. No closely similar extant genera were observed among these families, however.

Genus **FERRIGNOCARPUS** gen. nov.

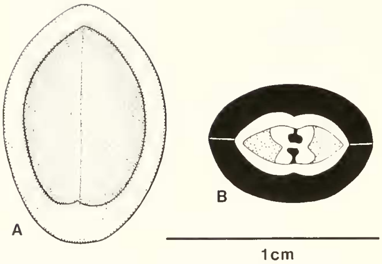
Etymology.—This genus is named for James P. Ferrigno, recognizing his services to paleobotany at the U.S. National Museum.
Type species.—*Ferrignocarpus bivalvis* sp. nov.

Ferrignocarpus bivalvis sp. nov.
Plate 49, figures 1–15, Text-figure 18

Etymology.—*Bi* (L = two) + *valva* (L = leaf of a folding door), referring to the two-valved structure of the endocarp.

Description.—Fruit unilocular, endocarp elliptical in face view, lensoidal in cross section, quadrilaterally symmetrical with two planes of symmetry intersecting at right angles in the vertical axis, base and apex rounded, endocarp length 4.5–9.0, avg. 6.3 mm (SD=1.48, n=19), width 3.4–6.4, avg. 4.7 mm (SD=0.81, n=18), thickness 2.1–3.9, avg. 2.9 mm (SD=0.57, n=17), bivalved, splitting along the major plane of symmetry, endocarp wall 1.0–1.2 mm thick, composed of: an inner layer about 50 μm thick composed of square to rectangular cells up to 15 μm in diameter, a middle layer typically 300 μm thick of vertically oriented fibers 25 μm in diameter, and a thick outer layer of anticlinally oriented short fibers, 55–75 μm long and 20–30 μm in diameter; rhomboidal crystals in idioblasts common at the contact between the two layers of fibers. Locule cast smooth, elliptical to broadly obcordate in face view, lensoidal to elliptical in cross section, quadrilaterally symmetrical, with a keel around the margin in the major plane of symmetry, and a shallow median longitudinal groove on both dorsal and ventral faces in the minor plane of symmetry; base slightly cordate or emarginate in face view, rounded in lateral view, sometimes with a thin straight stalk; apex obtuse in dorsiventral view, acute in lateral view.

Specimens.—Holotype: USNM 424624. Paratypes:



Text-figure 18.—*Ferrignocarpus bivalvis* gen. et sp. nov. **A**, Ventral view of a single fruit valve showing thick wall and concave locule. **B**, Typical specimen in transverse section.

UF 5669, 9386–9393, USNM 355348, 355369 (2 specimens), 355483 (8 specimens), 355404, 424803, 424804.

Discussion.—*Ferrignocarpus bivalvis* is represented mostly by locule casts that are distinctive in their cordate outline with a longitudinal keel in the major plane of symmetry and a longitudinal median groove in the minor plane of symmetry (e.g., Pl. 49, figs. 2–4, 7). Only a few of the locule casts retain some or all of the thick endocarp wall (Pl. 49, figs. 5, 6, 8, 9). One specimen is a mold in sandstone representing one valve of the endocarp pressed into the sediment showing the cordate outline of the locule within the elliptical outline of the endocarp (Pl. 49, fig. 1). The anatomy of the wall and locule contents are revealed in thin sections (Pl. 49, figs. 10–15). As seen in transverse sections, the locule contains an elliptical mass of parenchymatous tissue with a central 4-lobed space near the base (Pl. 49, figs. 12–14). The original structure is open to interpretation. The parenchymatous body may represent the storage tissue of a single seed with the 4-lobed central space representing the position of archegonia or of a decomposed embryo. The central part of the four-lobed space has an incomplete septum that appears to give rise to two placentae (Pl. 49, fig. 14).

Genus **FIMBRIALATA** gen. nov.

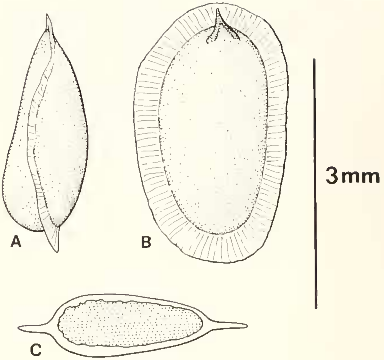
Etymology.—*Fimbria* (L = fringe) + *alatus* (L = winged).

Type species.—*Fimbrialata wingii* sp. nov.

Fimbrialata wingii sp. nov.

Plate 50, figures 14–19; Text-figure 19

Etymology.—This species is named after Scott L. Wing, recognizing his contributions to Eocene paleobotany.



Text-figure 19.—*Fimbrialata wingii* gen. et sp. nov. **A**, Seed in lateral view. **B**, Seed in face view showing the encircling wing. **C**, Transverse section of seed.

Description.—Seed subellipsoidal, asymmetrical, dorsiventrally compressed, consisting of a central seed body with a thin wing surrounding approximately in the dorsiventral plane; seed body more or less elliptical in cross-section, base and apex of seed and of seed body rounded in face view; seed height 2.9–3.7 mm, width 1.7–2.1 mm, thickness 0.6–0.9 mm; wing with striations oriented perpendicular to its margin, forming a flange about 0.3 mm wide around the seed body; surface of seed body smooth. Seed body with copious endosperm, embryo minute.

Specimens.—Holotype: USNM 435057. Paratypes: UF 6286, 6289, 6867, USNM 435058.

Discussion.—Because of the delicate nature of these fossils, the flanging wing often is partially broken. At first it appeared that the *Fimbrialata wingii* specimens might represent locule casts of a bivalved fruit with the "wings" representing the silica-filled crack along the dehiscence plane. However, transverse sections reveal a cutinized layer outlining a well-defined wing (Pl. 50, fig. 19).

Genus **FRAGARITES** gen. nov.

Etymology.—*Fragaria* (L = strawberry) + *ites* (Gr = like, having the nature of), referring to the similarity in shape to the achenes of *Fragaria*.

Type species.—*Fragarites ramificans* sp. nov.

Fragarites ramificans sp. nov.

Plate 50, figures 1–4

Etymology.—The epithet refers to the ramifying surface ribs.

Description.—Seed (or achene?) bilaterally symmetrical, laterally compressed and more or less D-shaped in the plane of symmetry, i.e., rounded in lateral outline except for the straight hilar margin, and lenticular in cross section; length along hilar margin 2.4–3.7, avg. 3.0 mm (SD=0.63, n=7), width 2.0–3.3, avg. 2.4 mm (SD=0.53, n=7), thickness 1.4–2.3, avg. 1.7 mm (SD=0.39, n=7), length/thickness ratio 1.6–1.9; upper end of the flat hilar margin with a micropylar point, lower margin of the flat hilar margin rounded, surface covered by a reticulum of bifurcating fibrous ribs ca. 0.1 mm in diameter that are oriented approximately at right angles to the hilar edge. Inner mold of seed coat similar in shape to the seed, with smooth surface.

Specimens.—Holotype: USNM 424729. Paratypes: UCMP 10745, UF 6421, 9557–9564.

Discussion.—*Fragarites ramificans* is represented by chalcedony casts of a seed or achene with prominent bifurcating ribs that run at right angles to the hilar edge (Pl. 50, figs. 1, 3). Most commonly, it is preserved as an inner mold of the seed coat, with little or none of the outer reticulum adhering. Internal anatomy has not been determined. At least superficially, these specimens with their D-shaped outline and transverse ribbing resemble achenes of *Fragaria* in the Rosaceae.

Genus **GLOBULICARPIUM** gen. nov.

Etymology.—*Globulus* (L = bead) + *karpos* (Gr = fruit).

Type species.—*Globulicarpium levigatum* sp. nov.

Globulicarpium levigatum sp. nov.

Plate 50, figures 5–13

Etymology.—*Laevis* (L = smooth), referring to the smooth surface of the fruit.

Description.—Fruit nearly spherical, but with the pedicel scar raised on a nipple-like projection, hence slightly longer than wide, unilocular, single-seeded, indehiscent, length 4.3–6.8, avg. 5.5 mm (SD=0.79, n=13), equatorial diameter 3.2–5.7, avg. 4.5 mm (SD=0.66, n=17); surface smooth, sometimes shiny; pericarp 0.9 mm thick, composed of at least four successive layers: 1) locule lining composed of a uni- to biseriate layer about 24 μm thick of thin-walled horizontally oriented cells 10–15 μm high by 50–87 μm long, 2) a thick layer, 400–500 μm thick, consisting of isodiametric to horizontally elongate thick-walled sclereids varying to large size (50–210 μm in diameter), often with dark contents, nested among horizontally elongate parenchyma cells 15–40 μm thick, 60–120 μm wide, this layer containing about 20 longitudinal vascular bundles with helically thickened elements situated about in the middle of the layer, the inner ¼ of the middle layer in most specimens usually poorly preserved, detail obscured by the confluence of the opaque contents of oil cells or sclereids; 3) a band 150–175 μm thick of isodiametric parenchyma cells 15–25 μm in diameter and, 4) a uniseriate outer layer of anticlinally elongate cells 35 μm high, 8–12 μm wide. Locule globose, smooth-walled, seed filling the locule, cotyledons not preserved.

Specimens.—Holotype: USNM 355663. Paratypes: UCMP 10623, UF 6349, 8804–8807, 9331, 9332, 9506–9512, USNM 435009–435011, 435038.

Discussion.—*Globulicarpium levigatum* is represented in the Nut Beds by casts and permineralized fruits. Although similar in size and globose shape to *Celtis* which is also common in the Nut Beds, it is distinguished in the field by its smooth outer surface and nipple-like attachment scar. Transverse and longitudinal sections have revealed the thickness and anatomy of the pericarp (Pl. 50, figs. 11–13). The pericarp was probably leathery; a few specimens are shriveled like a raisin (e.g., UF 9332).

The affinities of *Globulicarpium* could possibly be with the Lauraceae, but the lack of columnar cells, which are characteristic of the endocarps of Lauraceae (Reid and Chandler, 1933), and lack of preservation of large plano-convex cotyledons have made me hesitant to assign it to that family. This species appears to be very similar in external morphology to a specimen figured as "undetermined Lauraceae fruit" by Collinson (1983, fig. 216) from the London Clay flora, but I have not conducted a detailed comparison.

Genus **HEXACARPELLITES** gen. nov.

Etymology.—*Hexa* (Gr = six) + *karpos* (Gr = fruit), referring to the six carpels evident in this fruit.

Type species.—*Hexacarpellites hallii* sp. nov.

Hexacarpellites hallii sp. nov.

Plate 51, figures 1–4

Etymology.—This species is named after William and Gertrude Hall of Vancouver, Washington recognizing their encouragement and support of the Clarno paleobotany project.

Description.—Fruit subglobose, prolate, with six radially connate carpels, base and apex rounded, surface texture unknown; length 5.1 mm, equatorial diameter 4.3 mm; with six vertically elongate locules up to 4.5 mm high, 0.8 mm wide and 1.1 mm dorsiventral thickness; septa thick, with obvious suture lines; one seed per locule, placentation axile; seeds shrunken within locules, seed coat composed of a thin layer of polygonal to spherical, tan cells, 20–35 μm in diameter; apparent embryo within seed 0.41 mm thick dorsiventrally, 0.1 mm wide, preserved in dark brown silica; central axis of fruit thick and prominent from base to apex, filled with dark fibers and vascular tissue.

Specimen.—Holotype: USNM 424653.

Discussion.—*Hexacarpellites hallii* is represented by a single specimen. Although it appears to have a rough outer surface (Pl. 51, fig. 1), the exterior of the fruit is fragmented away, possibly having adhered to the sedimentary matrix from which it was collected, leaving no evidence of original surface detail. Serial sectioning, however, revealed very good internal preservation, including a seeds and embryo within each locule (Pl. 51, figs. 2–4). Successive transverse sections showed that the locules are axially elongate and single-seeded. The distal margin of each locule cast is exposed in a median longitudinal groove of the fruit. This may be an artifact of the way that the fossil was removed from the matrix, but if it is an original feature of the fruit it suggests that dehiscence was loculicidal.

Genus **JOEJONESIA** gen. nov.

Etymology.—Named after Joseph Jones III, director of Hancock Field Station, Fossil, Oregon, recognizing his support and encouragement of paleobotanical field studies at the Nut Beds.

Type species.—*Joejonesia globosa* sp. nov.

Joejonesia globosa sp. nov.

Plate 51, figures 5–8

Etymology.—*Globus* (L = ball), referring to the fruit shape.

Description.—Fruit globose, unilocular, bivalved, height 8 mm (est.), equatorial diameter 8.0 mm, with a reticulum of thin veins over the surface; endocarp wall 1.3 mm thick, composed of isodiametric subangular sclereids typically 90–150 μm in diameter, smaller toward the locule (40–60 μm), locule lining uniseriate, composed of poorly preserved rectangular cells, 40 μm thick; locule smooth, with a keel in the plane of dehiscence.

Specimen.—Holotype: UF 9260.

Discussion.—This species is represented by a single fragmentary specimen. It is sufficiently complete, however, to discern both internal and external morphology of the endocarp, and the anatomical preservation is excellent. The salient features of *Joejonesia* are globose shape, reticulate surface, bivalved endocarp (Pl. 51, fig. 5), the smooth, keeled locule (Pl. 51, figs. 6, 7) and the large sclereids composing the endocarp (Pl. 51, fig. 8). Although the locule in this specimen is empty, its form suggests that there was only a single seed. In size and bivalvate construction, it brings to mind *Prunus*, but *Prunus* has smaller sclereids composing the wall and the dehiscence plane is developed on only one side of the endocarp (cf. Pl. 35, figs. 11–15).

Genus **LIGNICARPUS** gen. nov.

Etymology.—*Lignum* (Gr = wood) + *karpos* (Gr = fruit).

Type species.—*Lignicarpus crassimuri* sp. nov.

Lignicarpus crassimuri sp. nov.

Plate 51, figures 9–16

Etymology.—*Crassi* (L = thick) + *murus* (L = wall).

Description.—Endocarp ovoid, elliptical to circular in cross section, unilocular, single-seeded, base and apex obtuse-rounded, length 9.7–11.4 mm, maximum width 6.0–6.1 mm, minimum width 3.7 mm; endocarp surface rough-textured, with longitudinally striate fibrous ribs, endocarp wall 1.4–2.0 mm thick, composed of longitudinally oriented fibers 50–88 μm diameter, with evenly distributed clusters (as seen in cross section) of smaller vertically oriented vascular strands; locule narrow-pyriform, rounded basally, tapering to a point apically. Seed pendulous?, conforming in shape to the locule, with a thin seed coat.

Specimens.—Holotype: UF 6111. Paratypes: UF 6578, 9765.

Discussion.—These thick-walled unilocular endocarps bear a superficial resemblance to those of *Nyssa*. However the fibers of *Lignicarpus crassimuri* run vertically, unlike those of *Nyssa* which form swirling tracts of varying orientation (cf. Pl. 11, fig. 19), and *Nyssa* does not have vascular bundles scattered through the endocarp.

Genus **LIGNIGLOBUS** gen. nov.

Etymology.—*Lignum* (L = wood) + *globus* (L = ball), referring to the woodiness and globose shape of the endocarp.

Type species.—*Ligniglobus sinuosifibrae* sp. nov.

Ligniglobus sinuosifibrae sp. nov.

Plate 53, figures 1–8

Etymology.—*Sinuosus* (L = full of bendings) + *fibra* (L = thread, fiber), referring to the sinuous arrangement of fibers over the surface of the endocarp.

Description.—Fruit subglobose, unilocular with a protrusion at one end, length 20.0–30.5 mm, equatorial diameter 20.0–25.1 mm; surface verrucate with fine, wavy, longitudinal striations; pericarp 4.2–6.3 mm thick composed successively of: 1) locule lining 120 μm thick, cells not well preserved, 2) main inner layer 3.7 mm thick of anticlinally oriented septate fibers 17–25 μm thick radiating outward from locule; 3) a 1.25 mm-thick zone of isodiametric parenchyma cells 50–80 μm in diameter; 4) an outer layer approximately 1 mm thick with periclinally and horizontally oriented fibers; 5) epicarp composed of periclinal files of rectangular cells 35–60 μm wide, 12–30 μm thick, apparently with ducts or vasculature running through this layer; locule globose to elongate.

Specimens.—Holotype: UF 8483. Paratypes: UF 8480, 9894, USNM 312752 (Bones, 1979, pl. 1, fig. 7), 354386.

Discussion.—*Ligniglobus* is represented by permineralized fruits that reveal woody internal structure in sections and fractured surfaces. Because of its relatively large size, thick wall, and single locule (Pl. 53, figs. 1–4), this fruit type is superficially similar to *Scabraecarpium clarnense* (cf. Pl. 59, figs. 1–7) but is distinguished by its more globose shape and finer, narrower endocarp fibers and by the lack of fibrovascular bundles in the endocarp.

Genus **LUNATICARPA** gen. nov.

Etymology.—*Lunat* (L = crescent moon) + *karpos* (Gr = fruit), referring to the crescent shaped outline of the fruit.

Type species.—*Lunaticarpa curvistriata* sp. nov.

Lunaticarpa curvistriata sp. nov.
Plate 52, figures 1–12

Etymology.—*Curvus* (L = bent) + *striata* (L = line), referring to the endocarp surface pattern.

Description.—Endocarp reniform, bilaterally symmetrical, laterally compressed in the plane of symmetry, unilocular, single-seeded; dorsal surface convex-rounded, with a rounded keel in the plane of symmetry, ventral side convex-rounded to nearly straight with a circular, centrally positioned funicular opening; dorsiventral length 2.6–4.9, avg. 3.7 mm (SD=0.51, n=32), width 3.2–5.0, avg. 4.1 mm, (SD=0.53, n=32), thickness 1.0–2.2, avg. 1.9 mm (SD=0.35, n=32); surface finely striate with the striations on the lateral faces arched parallel to the curvature of the dorsal surface; fruit surface following contour of the curved seed, and the bulging median condyle; pericarp 200–250 μm thick around the dorsal side, about five times thicker adjacent to the funicular opening, composed of: an inner layer 110 μm thick of isodiametric cells 12.5–30.0 μm in diameter and an outer layer 100 μm thick composed of fibers oriented parallel to the surface. Locule cast crescent-shaped to nearly straight, with a sharp median keel on the dorsal side and a ventral funicular plug, smooth to very faintly transversely ruminate, one of the limbs rounded, the other with a pointed tip. Seed curved, conforming to the shape of the locule.

Specimens.—Holotype: USNM 435020. Paratypes: UCMP 10717–10719, UF 6336–6341, 8582, 8767, 8773, USNM 355653, 422527, 422528, 435018, 435019, 435021, 435022, 435024–435037, 435045, 435046.

Discussion.—This species is represented by permineralized endocarps and numerous isolated locule casts. Distinctive endocarp features of *Lunaticarpa* are the reniform shape, dorsal keel, curved striations on the lateral faces (Pl. 52, figs. 1–3), and the large condylar cavity about which the locule is curved (Pl. 52, figs. 10, 11). The curvature and faint transverse ruminations of the locule cast bring to mind Menispermaceae. Similar, unornamented endocarps occur in extant *Pachygone*. However, this similarity may be the result of convergence; I have not been able to confirm affinities with Menispermaceae.

Genus **MICROPHALLUS** gen. nov.

Etymology.—*Micro* (Gr = small) + *phallus* (Gr), referring to the penial appearance of these specimens.

Type species.—*Microphallus perplexus* sp. nov.

Microphallus perplexus sp. nov.
Plate 53, figures 9–17

Etymology.—The epithet perplexus refers to the baffling affinities of this taxon.

Description.—Seed pyriform or tear-drop shaped in outline, bilaterally symmetrical, dorsiventrally compressed with a central depression (chalaza?) on the ventral surface, and a raised circular area (hilum?) on the dorsal surface; length of complete seed 4.8–6.7, avg. 5.5 mm (SD=0.45, n=7), width 3.2–4.7, avg. 3.8 mm, (SD=0.50, n=7), thickness 2.3–3.2, avg. 2.7 mm (SD=0.34, n=6); seed coat thick (0.6 mm) comprised of a uniseriate layer of elongate thick walled cells which form coarse surface striations that radiate from the periphery of the dorsal raised area and the from the center of the ventral face. Embryo forming a circular loop in the main seed body, and a pronounced apical extension (radicle) about 0.7 mm in diameter and up to 2 mm long that protrudes through the apex of the seed; length of embryo cast 4.4–6.3, avg. 5.5 mm (SD=0.72, n=5), width 2.5–3.2, avg. 2.8 mm (SD=0.27, n=5), thickness 1.2–1.6, avg. 1.4 mm (SD=0.15, n=5).

Specimens.—Holotype: UF 5243, complete seed. Paratypes: UF 6346, 9280, USNM 355414, 355391, 355685 (2 specimens), complete seeds; OMSI Pb1839, UCMP 10739, 10740, UF 5242, 9281, 9282, USNM 355685 (3 specimens), 434965, embryo casts.

Discussion.—Seeds of *Microphallus* present a distinctive morphology and are easily recognized because the embryo, usually preserved in white chalcedony, resembles a screw eye (Pl. 53, fig. 13). The loop in the embryo cast may represent curved cotyledons, but in most specimens the loop is closed with no indication of where the cotyledons might terminate. I interpret the raised dorsal area on the seed (Pl. 53, figs. 10–12, 15, 16) to be the hilum and the ventral cavity (Pl. 53, figs. 9, 14) to be the chalaza, but as yet, I have no clue as to the systematic affinities of this fossil.

Genus **NEPHROSEMEN** gen. nov.

Etymology.—*Nephro* (Gr = kidney) + *semen* (L = seed) referring to the roughly kidney-shaped outline of the seed.

Type species.—Nephrosemen reticulatus sp. nov.

Nephrosemen reticulatus sp. nov.
Plate 54, figures 6–13

Etymology.—reticulatus (L = netlike), referring to the seed surface pattern.

Description.—Seed reniform, bilaterally symmetrical, laterally compressed in the plane of symmetry, more or less rounded in lateral profile, with a concave notch at the hilar end, micropyle pointed, situated adjacent to hilum; seed height (hilum to dorsal edge) 2.2–3.1, avg. 2.7 mm (SD=0.28, n=19), width 2.2–3.0, avg. 2.5 mm (SD=0.23, n=19), thickness 1.1–1.9, avg. 1.3 mm (SD=0.20, n=19); smoothly contoured, surface covered by a fine reticulum of pentagonal and hexagonal cells 49–62 μm in diameter with thick anticlinal walls, these cells aligned in rows radiating from the micropyle area.

Specimens.—Holotype: UF 6500. Paratypes: UF 6389, 6573, 9167, 9376–9382, USNM 355047, 355052, 355403, 424683–424686, 424746–424749.

Discussion.—Nephrosemen is readily recognized in the Nut Beds collections by the kidney-shaped lateral profile, lateral compression and reticulate surface. Specimens vary from longer than wide (Pl. 54, figs. 6–9, to wider than long (Pl. 54, fig. 11). The closely adjacent hilum and micropyle (Pl. 54, fig. 7) suggest that the seed was anatropous. The seed shape and reticulate surface bring to mind seeds of extant Theaceae. They are much larger than the seeds of *Cleyera* (cf. Pl. 38, figs. 1–5), yet the surface reticulum (Pl. 51, fig. 10) is much finer, and a curved embryo has not been detected in *Nephrosemen*. There is an even closer resemblance to seeds of genera in the Solanaceae, for example, *Mandragora*, *Solanum* (part), *Physocarpus*, in the shape and reticulate surface of the seed. Whether the embryo is curved or coiled in the fossil, as in Solanaceae, remains undetermined.

Genus **OMSICARPIUM** gen. nov.

Etymology.—This fruit genus is named for OMSI, the Oregon Museum of Science and Industry, recognizing the role of this museum in supporting this project.

Type species.—Omsicarpium striatum sp. nov.

Omsicarpium striatum sp. nov.
Plate 52, figures 13–16

Etymology.—Stria (L = furrow, line) referring to the striated endocarp surface.

Description.—Fruit pyriform, more or less circular in cross section, base and apex rounded, unilocular; height 33.5 mm, width 20.0 mm; ornamented with prominent, sinuous, closely spaced longitudinal striations, pericarp 2.4 mm thick, with an apparent longitudinal suture on one side, anatomy and seed structure not preserved.

Specimen.—Holotype: OMSI Pb265.

Discussion.—This specimen is preserved in calcite, without cellular details. The surface detail is well preserved, and the specimen is clearly unilocular with a relatively thick wall. In general form it is similar to *Pruniticarpa*.

Genus **PASTERNACKIA** gen. nov.

Etymology.—Named for Ellen Pasternack recognizing her assistance in collecting at the Nut Beds.

Type species.—Pasternackia pusilla sp. nov.

Pasternackia pusilla sp. nov.
Plate 55, figures 1–4

Etymology.—The epithet *pusilla* (L = very little) refers to the small size of these seeds.

Description.—Seed anatropous, ovoid, bilaterally symmetrical, nearly circular in transverse section, tapering gradually to the acute hilar/micropylar end, rounded-obtuse at the opposite end; length 1.1–1.2, avg. 1.1 mm (SD=0.05, n=5), width 0.7–0.8, avg. 0.74 mm (SD=0.05, n=5); surface reticulate, formed by 16 to 22 meridionally aligned rows of cells with thickened anticlinal walls, these cells four- to five-sided in surface view; the rows of cells along the raphal side (?) narrower than those over the rest of the seed surface.

Specimens.—Holotype: UF 9604. Paratypes: UF 9605–9608.

Discussion.—Pasternackia seeds are preserved as small ovoid chalcedony casts with a distinctive reticulate surface formed by large, meridionally aligned seed coat cells (Pl. 55, figs. 1–4). There is a resemblance to seeds of *Saurauria* in the Actinidiaceae, but the meridional alignment of cells is more strongly asymmetrical. The hilar end is damaged in each of the fossils so that the precise morphology of the hilum and micropyle could not be determined.

Genus **PILEOSPERMA** gen. nov.

Etymology.—Pileos (Gr = cap) + *spermum* (Gr = seed)

Type species.—Pileosperma minutum sp. nov.

Pileosperma minutum sp. nov.
Plate 55, figures 5–8

Description.—Seed pyriform, bilaterally symmetrical, rounded basally and laterally, seed broadest near the base with the wall tapering gradually toward the pointed micropylar end, abruptly more tapered near the apex to form a broad-conical tip, seed length 2.5–3.2, avg. 2.7 mm (SD=0.25, n=6), width in plane of symmetry 1.2–1.8, avg. 1.5 mm (SD=0.20, n=6), width at right angles to plane of symmetry 1.0–1.4, avg. 1.3 mm (SD=0.15, n=6); with a raised circular cap (chalaza?) at the base facing ventrally, surface microreticulate, made up of isodiametric polygonal cells 15–20 μm in diameter, sometimes with faintly superimposed impression of large meridionally arranged rectangular cells.

Specimens.—Holotype: UF 6606. Paratypes: UF 6425, 9588–9591; USNM 424784–424787.

Discussion.—These small seeds are preserved as chalcedony casts with well preserved cell outlines on the surface (Pl. 55, fig. 7). The raised circular basal cap (Pl. 55, figs. 5, 8) that may represent the chalaza is a conspicuous feature of this fossil genus. This cap is sometimes detached, but is still evident because of the scar left behind (Pl. 55, fig. 6). There is no obvious raphe, but there commonly is a broad, shallow ventral groove leading between the base and apex.

Pileosperma ovatum sp. nov.
Plate 55, figures 9–11

Description.—Seed pyriform, bilaterally symmetrical, pointed at the apical micropyle, rounded basally and laterally, broadest near the base, gradually tapered all the way to the apex, length 2.0–3.0, avg. 2.5 mm (SD=0.32, n=32), broadest width 1.5–2.2, avg. 1.9 mm (SD=0.19, n=33), narrowest width 1.3–2.0, avg. 1.6 mm (SD=0.16, n=33), with a raised circular cap (chalaza?) at the base. Surface microreticulate, made up of isodiametric polygonal cells 23–35 μm in diameter, sometimes with faintly superimposed impression of large meridionally arranged rectangular cells.

Specimens.—Holotype: USNM 424751. Paratypes: UF 6420, 6422–6423, 6499, 9722, 9723. USNM 424726, 424755, 424758, 424760, 424762, 424764, 424766, 424767, 424769–424783, 424787.

Discussion.—Although clearly congeneric with *Pileosperma minutum*, *P. ovatum* is distinguished by its broader shape, and by the uniform curvature of the lateral walls toward the apical tip.

Genus **PISTACHIOIDES** gen. nov.

Etymology.—*Pistachia* + *oides* (Gr = like, resembling), indicating the similarity to the common pistachio nut.

Type species.—*Pistachioides striata* sp. nov.

Pistachioides striata sp. nov.
Plate 54, figures 1–5

Etymology.—*Stria* (L = furrow, line), referring to the striated surface of the endocarp.

Description.—Fruit ovate in face view, nearly elliptical in lateral view, rounded-quadrangular in cross section, base rounded, apex pointed, bilaterally symmetrical, unilocular, length 21–24 mm, width across plane of symmetry 10.7–13.6 mm, dorsiventral thickness 8.7–14.2 mm, with a keel in the plane of symmetry showing a suture line along which two valves were probably joined; endocarp wall thin (0.4 mm), composed of diagonally oriented fibers, attachment scar elliptical, elongate in the plane of symmetry.

Specimen.—Holotype: USNM 422387. Paratype: UF 6440.

Discussion.—*Pistachioides* is represented by two endocarp casts from the Nut Beds. The holotype (Pl. 54, figs. 1–5) is replaced by chalcedony; the paratype is replaced by calcite. Characters of shape, size, keel and dehiscence plane coincident with the plane of symmetry, diagonally oriented surface striations, and the attachment scar which is elongate in the plane of symmetry, correspond closely to those of *Pistacia vera*, the commercial pistachio nut. The basal margin, as viewed laterally in the plane of symmetry, is oblique, as it is in *Pistachia*. I have hesitated to place it within this extant anacardiaceous genus because of the lack of corroborating anatomical details in the fossils. Internal anatomy is not preserved in the fossil specimens; the fossils, however, appear to have a fibrous outer layer, whereas the outer layer in *Pistacia* is formed by more or less isodiametric sclereids.

Genus **POLLOSTOSPERMA** gen. nov.

Etymology.—*Pollostos* (Gr = smallest, least) + *sperma* (Gr = seed), because these seeds are among the smallest from the Nut Beds.

Type species.—*Pollostosperma dictyum* sp. nov.

Pollostosperma dictyum sp. nov.
Plate 56, figures 9–12

Etymology.—*Diktyon* (Gr = net) referring to the reticulate surface of the seed.

Description.—Seed laterally compressed, wide-ovate in lateral view, lensoidal in transverse section, bilaterally symmetrical, length 1.1–1.3 mm, width 0.9–1.2 mm, thickness across plane of symmetry 0.6–0.9 mm, with a keel in the plane of symmetry, rounded basally and pointed apically as viewed laterally; surface reticulate, with cells ca. 50 μm in diameter.

Specimens.—Holotype: UF 9830. Paratypes: UF 9831–9840, USNM 355448.

Discussion.—This species is one of the more abundant seed types at the Nut Beds although it is easily overlooked in the field because of its small size. In many specimens the reticulate surface is damaged in the process of removal from the matrix. In sorting through numerous seeds of this type collected by Thomas Bones, however, a few specimens with well preserved external surface were found (e.g., Pl. 56, figs. 9–12). The affinities are still unknown.

Genus **POLYGRANA** gen. nov.

Etymology.—Poly (Gr = Many) + *granum* (Gr = seed), referring to the large number of seeds within this fruit type.

Type species.—Polygrana nutbedense sp. nov.

Polygrana nutbedense sp. nov.

Plate 56, figures 1–8

Etymology.—The epithet refers to the Nut Beds locality.

Description.—Fruit a subovoid, prolate, multiseeded berry with slight irregular depressions and bulges, roughly circular in cross section, length 9.1–10.1 mm, equatorial diameter 6.1–8.4 mm, perianth hypogynous; scar forming a persistent circular flange at the fruit base; fruit surface smooth, with occasional fine, unbranched longitudinal fibrovascular bundles; unilocular with many seeds; fruit wall ca. 0.4 mm thick, placentation apparently parietal, with seeds embedded in a tissue of parenchyma cells 50–240 μm in diameter, and/or with groups of narrow parallel fibers. Seeds ovoid, 1.0 mm long by ca. 0.5 mm in equatorial diameter, orthotropous (?), seed coat 40–60 μm thick with a conspicuous layer of about eight rows of anticlinally flattened polygonal cells, embryo straight.

Specimens.—Holotype: USNM 355493. Paratypes: UF 5665, 5673.

Discussion.—Polygrana is known only from a few permineralized multiseeded berries. The thin exocarp appears to have been leathery, and the mesocarp pulpy, resulting in distorted, somewhat squashed specimens (e.g., Pl. 56, fig. 6). The placentation apparently is parietal, although many of the seeds appear to be floating within parenchymatous tissue some distance from the margin (Pl. 56, figs. 5, 6). The number of carpels is uncertain. The fruits bear a resemblance to certain Flacourtiaceae, including *Banara*. I have not found a modern genus with a seed coat of conspicuously flattened polygonal cells like that of this fossil (Pl. 56, fig. 8).

Genus **PRUNITICARPA** gen. nov.

Etymology.—Prunus + *ite* (L, Gr = having the nature of) + *karpos* (Gr = fruit), referring to the general resemblance to extant *Prunus*.

Type species.—Pruniticarpa cevallosii sp. nov.

Pruniticarpa cevallosii sp. nov.

Plate 56, figures 13–16; Plate 57, figure 20

Etymology.—The epithet *cevallosii* is named in recognition of the contributions of Sergio Cevallos-Ferriz to fossil wood and fruit research.

Description.—Endocarp subpyriform, nearly circular in cross section, pointed apically and basally, bilaterally symmetrical, unilocular, single-seeded, length 39 mm, width 24 × 23 mm, surface rough, with a single low, rounded longitudinal ridge running from base to apex at the position of carpel closure in the plane of symmetry, endocarp wall 3.8–4.3 mm thick, composed of compact sclereids, grading from an inner layer of small isodiametric sclereids 20–38 μm in diameter through a middle layer with anticlinally elongate cells 100–150 μm long and 25–65 μm wide, to the outer part with large rounded isodiametric cells 37–75 μm in diameter; locule lining loosely adherent to the endocarp, composed of a three- to five-seriate layer of small globose cells, 20–30 μm in diameter, with a uniseriate layer of scattered rectangular peg-like cells 40–50 μm in diameter. Locule cast rounded basally, pointed apically with a longitudinal keel corresponding to the dehiscence line, 25.7 mm long, 7.7 mm wide.

Specimens.—Holotype: UF 9209. Paratypes: USNM 355194, 446087.

Discussion.—This large unilocular endocarp is known from only a few well preserved specimens. The holotype was sectioned transversely, showing the thick endocarp wall, nearly circular outline of the endocarp and locule and plane of dehiscence (Pl. 56, fig. 15). Although it resembles *Prunus* in having a thick-walled, woody, unilocular endocarp and plane of dehiscence running longitudinally on only one side of the fruit, I have not observed any extant species of *Prunus* with endocarps that are circular in cross section.

Genus **PTERONEPELYS** gen. nov.

Etymology.—Pteron (Gr = wing) + *epelys* (Gr = stranger).

Type species.—Pteronepelys wehrii sp. nov.

Pteronepelys wehrii sp. nov.

Plate 57, figures 1–3; Text-figure 20

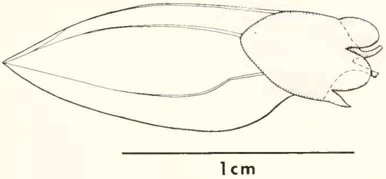
Etymology.—The species is named in honor of Wesley Wehr, who has provided excellent comparative material of this taxon from the Republic flora, Washington.

Description.—Samara consisting of a laterally flattened, ovoid endocarp with an elongate, more or less elliptical wing; samara length 10.0–13.9 mm, width 3.7–4.3 mm; endocarp length 3.5–4.5 mm, width 2.6–3.0 mm, thickness ca. 2–2.5 mm; wing with a straight to slightly convex upper margin and a convex lower margin joined distally in an acute angle, three longitudinal veins arising from the nutlet, joining at the distal tip of the wing: a thick vein closely following the upper margin of the wing, another thick vein situated between the midline of the wing and the upper wing margin, and a thin vein following the lower margin situated between the lower margin and midline of the wing; apex of nutlet, opposite the wing attachment, giving rise to four (or five?) stout sepals 1.5 mm high and 1.5 mm wide with rounded apices, and two central style arms.

Specimens.—Holotype: OMSI Pb1018. Paratypes: OMSI Pb1381, Nut Beds; UF 11696, Clarno White Cliffs locality; UWBM 36963, 36966, 36976, 36977, 54650, Republic flora.

Discussion.—This species is represented in the Nut Beds by a few specimens preserved as impressions in siltstone from the leaf layer of Face 3 (Pl. 57, figs. 1, 2). Although it has not been described previously, the same species is also known from the Clarno White Cliffs locality (Pl. 57, fig. 3) and from the Middle Eocene Republic flora of northeastern Washington (Wolfe and Wehr, 1987). Details of the sepals and styles are more clearly preserved in the specimens from Republic.

Superficially, *Pteronepelys* fruits resemble those of *Cedrelospermum* (cf. Pl. 43, figs. 16–18); however, *Pteronepelys* is distinguished by fewer veins in the wing, by the lack of a secondary wing, and the position of the perianth relative to the wing. The sepals protrude from the opposite side of the nutlet from the wing. From the orientation of the styles and perianth, it appears that the pedicel attachment was at the other end of the fruit, at the tip of the wing (Text-fig. 20).



Text-figure 20.—*Pteronepyles wehrii* gen. et sp. nov.

Genus **PULVINISPERMA** gen. nov.

Etymology.—*Pulvinis* (L = cushion, pad, pillow) + *spermum* (Gr = seed).

Type species.—*Pulvinisperma minutum* sp. nov.

Pulvinisperma minutum sp. nov.
Plate 57, figures 4–8

Etymology.—*Minutus* (L = small, little), referring to the seed size.

Description.—Seed more or less pillow-shaped, bilaterally symmetrical, laterally compressed with a keel in the plane of symmetry, rounded-rhomboidal in lateral view, more or less lensoidal in face view and in cross section, length 0.9–1.3, avg. 1.1 mm (SD=0.13, n=10), width in plane of symmetry 0.7–0.8, avg. 0.76 mm (SD=0.05, n=10), thickness across the plane of symmetry 0.5–0.7, avg. 0.56 mm (SD=0.07, n=10), rounded basally and apically, hilum and elliptical scar in the plane of symmetry at the junction of the apical and ventral margins; pointed, micropylar projection on the opposite side from the hilum at the junction of the apical and dorsal margins.

Specimens.—Holotype: UF 9740. Paratype: UF 9741–9743, 9841–9850.

Discussion.—This species is represented by numerous small chalcedony seed casts. Salient features include the rhomboidal outline in lateral view and keel in the plane of symmetry. The affinities remain unknown.

Genus **PYRISEMEN** gen. nov.

Etymology.—*Pyrum* (L = pear) + *semen* (L = seed), referring to the pear-like shape of the seed.

Type species.—*Pyrisemen attenuatum* sp. nov.

Pyrisemen attenuatum sp. nov.
Plate 57, figures 9–12

Etymology.—*Attenuatus* (L = drawn out, tapered), referring to the narrowed seed apex.

Description.—Seed/achene pyriform, asymmetrical, attenuate-pointed apically, rounded basally, laterally flattened, elliptical in cross section, length 2.4–4.3, avg. 3.1 mm (SD=0.58, n=9), width 1.2–3.5, avg. 1.3 mm (SD=0.91, n=9), thickness 1.8–2.3, avg. 2.1 mm (SD=0.19, n=9); base with a recessed circular scar, 0.8–1.0 mm in diameter, surface smooth. Inner body similar in shape to outer surface, forming a silhouette in translucent specimens.

Specimens.—Holotype: UF 6463. Paratypes: UCMP 10626–10629, UF 6400–6404, 6464–6466, USNM 355373, 355419 (6 specimens), 435049, 435059.

Discussion.—This species is usually preserved in white or translucent chalcedony. Although internal cell structure has not been preserved, some specimens show the silhouette of an internal seed coat in transmitted light (Pl. 57, figs. 11, 12). Possibly they are achenes tapering apically toward the style with the circular scar representing the pedicel attachment. Alternatively, they may represent bitegmic seeds with a circular basal hilum tapering toward the micropyle. Seeds that are at least superficially similar occur in the Flacourtiaceae, e.g., *Oncoba*.

Genus **QUINTACAVA** gen. nov.

Etymology.—*Quinta* (L = five) + *cavus* (L = hollow, hole), referring to the five prominent locules of the fruit.

Type species.—*Quintacava velosida* sp. nov.

Quintacava velosida sp. nov.
Plate 57, figures 13–19; Text-figure 21

Etymology.—*Velo* (L = cover, conceal) + *sidus* (L = star) referring to the star-shaped locule arrangement as seen in transverse section.

Description.—Fruit pentacarpellate, rounded-obconical, broadest basally, base more or less flat, with a circular pedicel scar in the center, apex rounded; length 6.9 mm, width 7.0–7.8 mm; central axis vascularized by a thin strand; five radially arranged, slender, elongate locules that are lanceolate in cross section alternating with large lacunae that are more or less triangular in cross section; lacunae occupying up to five times as much area as the locules, each locule separated from the adjacent lacuna by a thin wall, 0.15 mm thick, composed of five to twelve rows of axially oriented fibers 6–10 μm in diameter with scattered vertical resin or gum ducts, these ducts circular in cross section, 12–25 μm in diameter; locule lining composed of a uniseriate layer of fibers varying in orientation from nearly horizontal near the fruit axis to nearly vertical toward the periphery of the fruit; outer wall of fruit 0.56 mm thick composed of isodiametric parenchyma cells, 40–60 μm in diameter; seeds not observed.

Specimen.—Holotype: USNM 424805.

Discussion.—This species is represented by a single well-preserved specimen. In cross section the arrangement of locules resembles a five-rayed star (Pl. 57, fig. 16). The anatomy of the septa, with vertically oriented fibers and conspicuous longitudinal ducts (Pl. 57, figs. 17, 18) are distinctive for this species. The outer wall of the fruit was soft or spongy, made up of parenchyma (Pl. 57, fig. 19) and the hard, fibrous wall around each of the locules appears to have functioned as a pyrene with dorsal dehiscence; indeed, two of the locules have split along their midline on the distal side (Pl. 57, fig. 16). The number and arrangement of locules is consistent with fruits of the Maloideae subfamily of the Rosaceae (Rohrer et al., 1991); however, the affinities, whether in the Rosaceae or elsewhere, remain to be determined.

Genus **SAMBUCUSPERMITES** gen. nov.

Etymology.—*Sambucus* + *spermum* (Gr = seed) + *ites* (Gr = like, having the nature of).

Type species.—*Sambucuspermites rugulosus* sp. nov.

Sambucuspermites rugulosus sp. nov.
Plate 58, figures 10–14

Description.—Seed small, elliptical to obovate in face view, slightly tapered toward the hilum, rounded at the opposite end, dorsiventrally flattened, sometimes concave ventrally and convex dorsally, length 1.2–1.5, avg. 1.4 mm (SD=0.12, n=5), width 0.9–1.2, avg. 1.0 mm (SD=0.11, n=5), thickness 0.4–0.5, avg. 0.46 mm (SD=0.05, n=5); surface with irregular, wavy horizontal rugulae, six to seven rugulae from base to apex.

Specimens.—Holotype: UF 6424. Paratypes: OMSI PB1716 (3 specimens), UF 6396–6399, 6426–6428, USNM 353980 (4 specimens).

Discussion.—This species is preserved as small silicified seeds, readily recognized by the ovate to elliptical shape, prominent horizontal rugulae (Pl. 58, figs. 10–14) and dorsiventral compression (Pl. 58, fig. 14). The seeds resemble those of modern *Sambucus* in general morphology and outline of surface, including the rugulate sculpture and the small circular aperture at the hilum. *Sambucuspermites* differs from extant species of *Sambucus*, however, in its small size (modern species are about 3 mm long), and fewer rugulae. Seeds of the Recent species *S. nigra* L., *S. ebulus* L., *S. puchella*, with which the fossil was compared, are more elongate in outline and have more rugulations than the fossil. Internal anatomy of the fossils was not observed. The name *Sambucuspermites* indicates the morphological similarity to *Sambucus* seeds, but does not necessarily imply a close relationship.

Genus **SCABRAECARPIUM** gen. nov.

Etymology.—*Scabra* (L = rough, scabby) + *karpos* (Gr = fruit).

Type species.—*Scabraecarpium clarnense* sp. nov.

Scabraecarpium clarnense sp. nov.
Plate 59, figures 1–7

Etymology.—The epithet refers to the Clarno Formation.

Description.—Fruit ovoid to obovoid, circular to elliptical in cross section, unilocular, base and apex rounded to obtuse-pointed, sometimes with a large circular recessed scar at base, fruit length 32.0–43.5, avg. 37.3 mm (SD=3.92, n=7), minimum width 23.0–28.5, avg. 26.3 mm (SD=2.19, n=8), maximum width 26.4–34.5 avg. 31.4 mm (SD=4.36, n=8), surface warty, woody to abraded; wall thick (4.5–10.5 mm) consisting of three layers: 1) an inner layer of radially arranged files of anticlinally elongate rectangular thin-walled cells 15–50 μm wide, 50–250 μm high, successively wider cells occur distally, 2) middle layer of thicker-walled cells, also anticlinally elongate and arranged in radial files, cells rectangular, 30–75 μm wide, 50–150 μm high, 3) outer layer of isodiametric parenchyma cells 50–70 μm in diameter; fibrovascular bundles 300–400 μm in diameter common, running obliquely with sinuous course through the middle layer and vertically through the outer parenchyma layer; locule circular to elliptical in cross section, 8–11 mm in diameter.

Text-figure 21.—*Quintacava velosida* gen. et sp. nov., fruit in transverse section showing five locules, large lacunae, and relatively thick outer wall.

Specimens.—Holotype: USNM 355066. Paratypes: UF 8481, 8482, USNM 354200, 354201, 354385, 354421, 354667, 422397, 424811.

Discussion.—*Scabraecarpium* is a thick-walled unilocular fruit type that is among the larger fruit types from the Nut Beds. The fruit wall is usually permineralized, and appears to have had a woody texture. Specimens vary from circular (Pl. 59, figs. 2, 5) to elliptical (Pl. 59, figs. 4, 6) in cross section. The fruit wall is similar in the anticlinal arrangement of fibers to that of *Ligniglobus* (Pl. 53, figs. 5–8); however, these fruits have a scabrate to verrucate surface texture, and the pericarp is composed of wider files of cells and has abundant large fibrovascular bundles in the pericarp (Pl. 59, fig. 7). Woody, unilocular fruits with abundant fibrovascular bundles occur in the Palmae. A detailed comparative survey has not been completed.

Genus **SCALARITHECA** gen. nov.

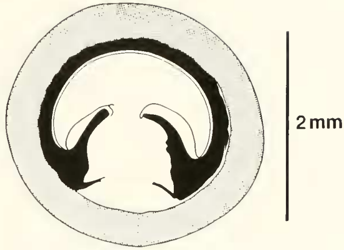
Etymology.—*Scalaris* (L = of a ladder) + *thecium* (L = case).

Type species.—*Scalaritheca biseriata* sp. nov.

Scalaritheca biseriata sp. nov.
Plate 58, figures 1–9

Etymology.—*Bi* (L = two) + *series* (L = row, succession), referring to the two rows of seeds.

Description.—Fruit ellipsoidal, bilaterally symmetrical, rounded apically and basally, length 4.7–6.0, avg. 5.0 mm (SD=0.55, n=7), width 3.0–3.4, avg. 3.1 mm (SD=0.2, n=4), thickness 2.8–4.2, avg. 3.6 mm (SD=0.57, n=5), fruit bilocular with a thick (0.8–1.0 mm) median hollow septum separating two rows of elongate seeds oriented with their long axes perpendicular to the long axis of the fruit; fruit wall smooth, 0.3–0.4 mm thick, without obvious sclerenchyma; septum rounded ventrally, thickening toward one end; seeds elongate, somewhat curved (concave against the septum), subcircular to oval in cross section, 2.0–2.4 mm long, 0.5–0.9 mm wide.



Text-figure 22.—*Scaphicarpium radiatum* gen. et sp. nov., fruit in transverse section showing mesocarp (grey), endocarp (black), with a large placentae and central seed.

Specimens.—Holotype: UF 5674. Paratypes: UF 6107, 6281, 8779, 8780, 9603, USNM 355680, 422530, 435087.

Discussion.—These silicified structures are interpreted as bilocular fruits with two rows of elongate seeds. The familial affinities, however, remain uncertain. The rows of seeds are visible both in longitudinal sections (Pl. 58, figs. 2–4) and in fractured specimens (Pl. 58, figs. 1, 6–9). The possibility was considered that this species might represent sporocarps of the fern *Marsilea*, with the elongate bodies representing sporangia, rather than seeds. However, thin sections failed to reveal any spores, and the anatomy of the sporangial walls in *Marsilea*, with anticlinally arranged cells, is unlike that of the seed coats in this fossil, which have periclinally arranged cells. The possibility also exists that the fruit-like organ may represent an insect egg case, and that the ellipsoidal structures are eggs rather than seeds. A throrough comparative check of extant insect egg cases was not included in this study.

Genus **SCAPHICARPIUM** gen. nov.

Etymology.—*Skaphe* (Gr = hollowed out like a boat) + *karpos* (Gr = fruit), referring to the boat-shaped locule casts of this fruit.

Type species.—*Scaphicarpium radiatum* sp. nov.

Scaphicarpium radiatum sp. nov.
Plate 59, figures 8–17; Text-figure 22

Etymology.—The epithet *radiatum* refers to the manner in which fruits radiate from the peduncle.

Description.—Infructescence a globose head of about twenty sessile fruits, head measuring 20 mm in diameter; fruit unilocular, single-seeded, ellipsoidal, with rounded base and apex, about twice as long as wide, circular in transverse section, length 4.7–7.2, avg. 5.5 mm (SD=0.87, n=8), width 2.6–3.3, avg. 2.7 mm (SD=0.80, n=8), thickness 1.9–2.6, avg. 2.2 mm (SD=0.28, n=7); pericarp composed of four layers: 1) main part of the endocarp wall 200 μm thick, composed of fibers 10–30 μm in diameter and more than 100 μm long that are arranged in tracts ranging from longitudinal to transverse in orientation; 2) uniseriate outer layer of the endocarp, composed of rectangular cells 50 μm high, 20–30 μm wide; 3) mesocarp 300–450 μm thick, composed of rounded thin-walled isodiametric to somewhat elongate parenchyma cells typically 30–60 μm in diameter, without ducts or obvious vascular tissue; 4) exocarp not preserved. Locule cast boat-shaped, rounded-basally, pointed apically, convex dorsally, concave ventrally, smooth, without a median keel, with a prominent circular placental scar central on the ventral face.

Specimens.—Holotype: USNM 312750 (Bones, 1979, pl. 6, fig. 5). Paratypes: UF 9523, 9525, USNM 355368, isolated endocarps; UF 5238 (Bones, 1979, pl. 6, fig. 3), 6322, 6324, 6328, 6334, 6359–6363, USNM 355458 (2 specimens), 355460 (7 specimens), 424701, 424731, 446056, 446061, locule casts.

Discussion.—*Scaphicarpium* occurs in the Nut Beds as permineralized fruits and isolated locule casts. The holotype is a silicified infructescence in siltstone matrix fractured and showing four attached fruits, plus the attachment scars of five more (Pl. 59, fig. 8). Although much of the infructescence is hidden with sediment, it may be estimated that the full head bore about twenty fruits. One fruit from this specimen was removed to reveal the locule cast (Pl. 59, figs. 9–12), and was sectioned transversely (Pl. 59, fig. 13), enabling recognition of detached endocarps and locule casts, which are relatively common in the Nut Beds. Some of the isolated specimens proved to be well preserved anatomically, and revealed anatomy of the endocarp and mesocarp (Pl. 59, fig. 14–16).

The boat-shaped locule casts (Pl. 59, figs. 9–13, 17) bring to mind Menispermaceae; however, the lack of a median keel, and the central, rather than subapical, placenta excludes this family. *Cantleya* in the Icacinaceae also has boat-shaped locules, but the endocarp in this genus is two-valved, whereas that of the fossil is undivided. I have also considered a possible relationship to the Cornales. Fruits in this order are commonly clustered, may be unilocular, and sometimes have a boat-shaped locule cast (e.g., *Mastixia*). However, the prominent centrally positioned circular placental scar (Pl. 59, fig. 17) and apparent lack of a dehiscence valve is inconsistent with the mastixioids.

Genus **SPHAEROSPERMA** gen. nov.

Etymology.—*Sphaero* (Gr = ball) + *spermum* (Gr = seed).

Type species.—*Sphaerosperma riesii* sp. nov.

Sphaerosperma riesii sp. nov.
Plate 58, figures 15–17

Etymology.—The epithet recognizes the contributions of John and Brian Ries to paleobotanical field work in the Clarno Formation.

Description.—Fruit spherical, 24.6–28.5 mm in diameter, surface smooth, pericarp 1.2–1.4 mm thick and composed of: 1) a locule lining about 100 μm thick of thick-walled rectangular to columnar sclereids, typically oriented with their long axes anticlinal and 2) a thick layer of rounded, elongate interdigitating cells profusely pitted with elliptical pits where they contact each other, with intracellular spaces; seed coat thin, embryo with two large hemispherical cotyledons.

Specimens.—Holotype: UF 9746. Paratype: UF 9599.

Discussion.—*Sphaerosperma* is represented by two specimens, both of which are embedded in hard tuffaceous matrix so that the outer shape is apparent only by fractures and sections (Pl. 58, figs. 15, 16). The holotype appears to show two hemispherical cotyledons. It is similar in shape and size to *Coryloides*, but has a smooth, rather than ribbed outer surface, lacks the cupule scar, and has a wall that is anatomically preserved, evidently more resistant to decay than that of *Coryloides*. The interdigitating cells composing the endocarp wall resemble those of *Palaeophytocrene* (cf. Pl. 58, fig. 17 and Pl. 20, fig. 5), but whether this is an indication of Icacinaceous affinity, or simply a case of convergence, or has not been determined.

Genus **SPHENOSPERMA** gen. nov.

Etymology.—*Spheno* (Gr = wedge) + *spermum* (Gr = seed).

Type species.—*Sphenosperma baccatum* sp. nov.

Sphenosperma baccatum sp. nov.
Plate 60, figures 7–10; Text-figure 23

Etymology—The epithet is derived from *bacca* (L = berry).

Description.—Fruit subglobose, prolate, circular in cross section, length 13 mm (est.), equatorial diameter 9.2 mm, surface smooth, unilocular with three partial septa 200–500 μ thick extending from the periphery of the fruit almost to the central axis, without an obvious central column, and with six radially arranged wedge-shaped seeds (five fully developed, one small); pericarp 200–300 μ thick, of two layers: 1) the inner ⅓ to ½ with horizontally oriented fibers 15–25 μm wide, 2) the ⅔ to ½ with anticlinally oriented fibers 12–15 μm wide. Seeds nearly triangular in cross section, with a convex dorsal surface and straight ventral sides that meet at 65–85°, with a "swelling" along the ventral side containing the raphe, seed height similar to that of fruit, width 3.3–4.2 mm, dorsiventral thickness 3.3–4.2 mm; seed coat 200 μm thick consisting of two layers: 1) the inner layer five- to seven-seriate, composed of rounded more or less isodiametric cells 20–50 μm in diameter, 2) the outer layer uniseriate, composed of large, columnar, anticlinally oriented cells 80–120 μm high, 25–45 μm wide with concave outer walls, giving the outer surface of the seeds a scalloped appearance.

Specimen.—Holotype: UF 5666.

Discussion.—*Sphenosperma* is known from a single specimen that was exposed in fracture planes through indurated siltstone, so that the exterior surface could not be photographed directly. The pieces were glued together so that the fruit could be sectioned transversely (Pl. 60, figs. 7–10). Successive serial sections revealed the morphology described above.

Important features of this taxon include the three septa (suggesting a tricarpellate fruit) and the wedge-shaped seeds with the punctate surfaces due to collapsed external walls of the outer layer of seed coat. I suspect that the number of seeds per fruit was variable in this species. In this specimen there are three seeds (including one that is abortive) between two adjacent septa, but only two and one seed are situated, respectively, between the other two pairs of adjacent septa.

Genus **STOCKEYCARPA** gen. nov.

Etymology.—This genus is named for Ruth A. Stockey, recognizing her contributions to paleobotany.

Type species.—*Stockeycarpa globosa* sp. nov.

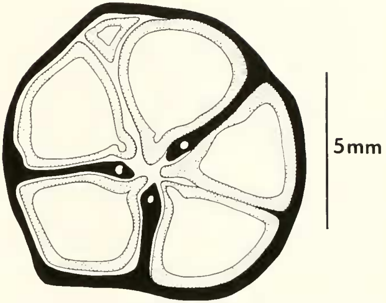
Stockeycarpa globosa sp. nov.
Plate 60, figures 11–14

Etymology.—*Globus* (L = ball), referring to the fruit shape.

Description.—Fruit spherical, unilocular, base and apex rounded, 6.8 mm in diameter, smooth-walled; inner layer composed of anticlinally elongate columnar cells 40–45 μm high, 6–8 μm wide, middle layer 400–500 μm thick composed of parenchyma apparently with intracellular spaces, outer preserved layer 300 μm thick, uniseriate, composed of anticlinally oriented fibers 300 μm high, 25–38 μm wide.

Specimen.—Holotype: UF 9747.

Discussion.—*Stockeycarpa* is represented by a single specimen in the Nut Beds. Although the seed is not preserved, the fruit anatomy is distinctive with the two layers of anticlinally elongate cells separated by a parenchymatous mesocarp (Pl. 60, figs. 13, 14). Another specimen that appears to be virtually identical morphologically and anatomically has been recovered in the Eocene Princeton Chert of British Columbia (Cevallos-Ferriz, pers. comm., 1992).



Text-figure 23.—*Sphenosperma baccatum* gen. et sp. nov., transverse section of the fruit showing six seeds (one small, perhaps abortive), and three intruding partial septae.

Genus **STRIATISPERMA** gen. nov.

Etymology.—*Stria* (L = line, furrow) + *sperma* (Gr = seed).

Type species.—*Striatisperma coronapunctatum* sp. nov.

Striatisperma coronapunctatum sp. nov.
Plate 60, figures 1–6

Etymology.—*Corona* (L = crown) + *punctum* (L = small hole, dot).

Description.—Seed globose to ellipsoidal, sometimes unevenly contorted or compressed, typically circular in cross section, rounded apically and basally, length 4.1–9.6 (–14.0) , avg. 6.1 mm (SD=1.45, n=59), equatorial diameter 2.7–8.5 (–11.2), avg. 5.7 mm (SD=1.20, n=58), with a circular scar at base and a small projection at the apex encircled by a cycle of about ten small circular to elliptical protrusions or depressions 60–100 μm in diameter, surface prominently striate with longitudinal rows of rectangular cells 8–11 μm in diameter, outer striate layer sometimes partially broken away and revealing another similarly striate surface with the same cell pattern. Sometimes with funicle or placental strands linking two or more seeds.

Specimens.—Holotype: USNM 424694. Paratypes: OMSI Pb271, UCMP 10624, 10625, UF 6325, 6335, 6455, 8700–8727, 8809–8815, 9211, 9212, USNM 355053 (3 specimens), 355054 (2 specimens), 355064–

355068, 355069 (4 specimens), 355070 (5 specimens), 355071, 355633, 422385, 424695, 424696, 424873, 435055, 435056.

Discussion.—*Striatisperma* seeds are relatively common at the Nut Beds. They are distinctive because of the outer surface of longitudinally aligned rows of square to rectangular cells (Pl. 60, figs. 1–6), and the ring of circular protrusions or scars surrounding the apex. The function of the circular scars is not known. Although typically more or less ellipsoidal and about 6 mm long, the seeds are variable in shape and size, some specimens being more than a centimeter in length. One specimen, UF 6455, is particularly large, 14.0 mm long, 10.0 × 11.2 mm wide. Although some examples have been sectioned and some are broken, no internal tissue has been observed beneath the two outer layers of longitudinally aligned cells. One specimen shows two silica seed casts partially embedded in matrix, linked by the silica cast of a bent, cylindrical funicle or placental strand (Pl. 60, fig. 5).

Genus **TENUISPERMA** gen. nov.

Etymology.—*Tenuis* (L = thin) + *spermum* (Gr = seed), referring to the thinness of the seed.

Type species.—*Tenuisperma ellipticum* sp. nov.

Tenuisperma ellipticum sp. nov.
Plate 61, figures 1–9

Etymology.—*Ellipsis* (L = a defective circle; ellipse) referring to the seed outline.

Description.—Seed elliptical in face view, dorsiventrally flattened and somewhat sinuous or wavy, base rounded, apex pointed; length 6.3, 10.5 mm, width 5.5, 7.2 mm, thickness 2.0, 2.0 mm, seed coat smooth, 250 μm thick, with an inner uniseriate layer of anticlinally elongate columnar cells 120–140 μm high, 30–60 μm wide and an outer three- to four-seriate layer composed of isodiametric sclereids, 30–40 μm in diameter; lateral margin with a grooved ridge extending from a point 2 mm from the apex on one side around the base and up to the position near the apex on the opposite margin of the seed.

Specimens.—Holotype: UF 6108. Paratype: UF 9528.

Discussion.—*Tenuisperma* seeds are preserved as white chalcedony seed casts. A ridge on the lateral margin has a median groove passing from near the apex on one side, over the base and to near the apex on the opposite margin of the seed. This groove terminates just prior to the top of the ridge, giving the appearance of a doubled, U-shaped structure (Pl. 61, fig. 4). This structure may represent the edges of the two cotyledons that are planar and closely adpressed to one another. Thus the seed is exalbuminous, filled by the embryo.

Genus **TIFFNEYCARPA** gen. nov.

Etymology.—Tiffney + *karpos* (Gr = fruit). The genus is named in honor of Bruce H. Tiffney, paleocarpologist.

Type species.—*Tiffneycarpa scleroidea* sp. nov.

Tiffneycarpa scleroidea sp. nov.
Plate 62, figures 1–7

Etymology.—*Skleros* (Gr = hard, tough), referring to the woodiness of the fruit.

Description.—Fruit subglobose, prolate, loculicidal capsule; base bluntly rounded with a central depression 0.95 mm in diameter; apex unknown, length 13 mm, equatorial diameter 9.5 mm; surface with longitudinal ribs and grooves, fruit woody, thick-walled with ten radially fused carpels and eight developed locules, each with a single seed; central axis with about ten vascular bundles alternating with the locules; locules vertically elongate, up to ca. 8 mm high, 0.8–1.3 mm wide, 1.7–2.3 mm dorsiventral dimension, locule lining uniseriate, composed of fibers 15–20 μm in diameter; endocarp composed mostly of equiaxial sclereids with undulating margins, 50–80 μm in diameter; radial planes of dehiscence formed by smaller sclereids radiating from the central axis and bisecting each locular area; exocarp (or possibly mesocarp) forming a band 400–500 μm thick of anticlinally oriented polygonal cells of variable size 40–120 μm radial dimension, 30–80 μm wide. Seeds attached to the ventral margin of the locule near the apex, embryo straight.

Specimen.—Holotype: USNM 355645.

Discussion.—*Tiffneycarpa* is known only from a single specimen that shows evidence of predepositional waterwear (Pl. 62, figs. 1–3). It is partially broken and replaced with silicified sandstone. Although the apex is missing, anatomical preservation is excellent, as seen in serial transverse thin sections (Pl. 62, figs. 4–7).

Distinctive features of this fruit are the woodiness, ten carpels, subapical axile placentation, and loculicidal planes of dehiscence (or carpel fusion) that extend fully from the axis to the endocarp periphery (Pl. 62, figs. 5–7). The morphology and anatomy are reminiscent of the extinct genera *Wetherelia* and *Palaeowetherelia* (see Mazer and Tiffney, 1982). However, these genera have both loculicidal and septicidal dehiscence.

Genus **TRIGONOSTELA** gen. nov.

Etymology.—*Trigono* (Gr = triangular) + *stele* (Gr = column).

Type species.—*Trigonostela oregonensis* sp. nov.

Trigonostela oregonensis sp. nov.
Plate 61, figures 10–18

Etymology.—The epithet refers to Oregon.

Description.—Fruit elongate, tricarpellate, trisymmetrical with three planes of symmetry intersecting in the long axis, lateral walls disposed in a trigonal prismatic pattern, trigonal in cross section, oblong in longitudinal view, apex pointed, base blunt, length of complete fruit 5.5–6.1, avg. 5.8 mm (SD=0.28, n=4), width 2.6–2.9, avg. 2.7 mm (SD=0.13, n=4); length of locule cast 4.8–5.4, avg. 5.2 mm (SD=0.32, n=3), width 1.7–2.0, avg. 1.9 mm (SD=0.17, n=3); three lateral faces joining to form longitudinal ribs, each of the three faces with a median groove corresponding to the position of a septum.

Specimens.—Holotype: USNM 424671. Paratypes: UF 6297, USNM 354599, 355643, 424672–424675, 435042.

Discussion.—*Trigonostela* is represented by silica casts and partial permineralizations. The elongate trigonal form of this fruit (Pl. 61, figs. 10–16) is very distinctive; however, the affinities have not been determined. One of the specimens sectioned transversely shows three septa that intrude inward, but which do not intersect, indicating a unilocular fruit (Pl. 61, fig. 17). Another specimen that was sectioned transversely appears to be composed of radiating fibers with poorly developed locules (Pl. 61, fig. 18). The anatomy and number of seeds per locule are not known.

Genus **TRIPARTISEMEN** gen. nov.

Etymology.—Tripart (three-parted) + *semen* (L = seed).

Type species.—*Tripartisemen bonesii* sp. nov.

Tripartisemen bonesii sp. nov.

Plate 62, figures 8–15

Etymology.—This species is named after Thomas J. Bones, who collected most of the specimens.

Description.—Seed subglobose, bilaterally symmetrical, dorsal surface rounded, ventral side with two facets joining at ca. 110° to form a median longitudinal crest in the plane of symmetry; with a pair of longitudinal keels formed at the junction of the ventral facets with the dorsal surface (In cross section subtriangular with a rounded dorsal side and a pair of straight ventral sides); base rounded, with a small circular hilar scar, apex pointed; seed length 2.8–4.4, avg. 3.5 mm (SD=0.41, n=31), width across plane of symmetry 2.6–4.3, avg. 3.4 mm (SD=0.43, n=31), thickness 2.1–3.5, avg. 2.8 mm (SD=0.35, n=20); seed coat smooth, septum 100–200 μm thick, Y-shaped, dividing the seed into three chambers: a pair of large, apparently empty, lateral chambers and a slender median, dorsal embryo chamber; embryo chamber sickle-shaped, curved in the plane of symmetry, with a flattened, rounded-triangular facet at the base, possibly the chalaza or a germination valve; septum formed of small isodiametric cells 12–20 μm in diameter, with an outer layer of cuboidal to rhomboidal thin walled cells 8–10 μm thick.

Specimens.—Holotype: UF 9288. Paratypes: UCMP 10741–10742, UF 9289–9316, 9577, 9578, 9734 (100 in lot), USNM 354484 (4 specimens), 354485 (18 specimens), 354486 (84 specimens), 354487 (4 specimens), 354488, 355688 (in matrix), 355395 (14 specimens), 355445 (5 specimens), 355688 in matrix.

Discussion.—*Tripartisemen bonesii* is one of the most abundant species in the Nut Beds, yet it is not known from other localities of the Clarno Formation or elsewhere in North America. It is often preserved as casts of the three chambers which may easily fall apart when the specimen is exposed. Permineralized seeds have been sectioned to reveal anatomy of the walls and septa (Pl. 62, figs. 14, 15). Sometimes the lateral chambers are filled with sediment, suggesting that they were originally empty, but had ruptured. The central chamber is generally filled with translucent silica, not clastic sediment, and in at least one instance (Pl. 62, fig. 15), preserves an embryo.

Collinson (1988) illustrated this type of seed both from the Nut Beds and from the Eocene of Messel, Germany. Although the well-preserved, lignitized Messel specimens differ in the nature of their preservation from the silicified Clarno seeds, the morphology appears to be identical. Collinson (1988 and work in progress) suggests possible lythraceous affinities for this genus. *Tripartisemen* resembles the extinct lythraceous genus *Mneme* Eyde in symmetry and presence of a median and two lateral chambers. However, there are a number of differences, including that *Mneme* seeds are about half as large, the embryo chamber is larger than the lateral chambers, and the lateral chambers are relatively thick-walled and are open along median slits (Friis, 1985).

Genus **TRIPLASCAPHA** gen. nov.

Etymology.—*Tripla* (L = triple) + *scapha* (L = small boat), referring to the three boat-shaped locules of the fruit.

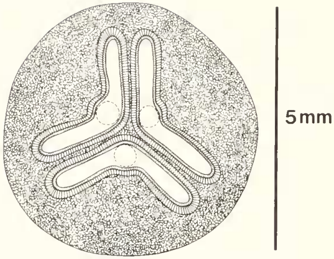
Type species.—*Triplascapha collinsonae* sp. nov.

Triplascapha collinsonae sp. nov.

Plate 63, figures 1–12; Text-figure 24

Etymology.—The epithet recognizes the important contributions of Margaret E. Collinson to paleocarpology.

Description.—Fruit ovoid, tricarpellate, trisymmetrical, nearly circular in cross section, one end (base?) rounded, the other (apex?) truncate with a circular disk; fruit length 4.0–6.0 mm, equatorial diameter 3.7–5.5 mm, trilocular with a single seed per locule; locule casts shallowly c-shaped in cross section, the ventral face



Text-figure 24.—*Triplascapha collinsonae* gen. et sp. nov., transverse section showing three seeds within parenchymatous pericarp.

convex, the dorsal face concave, 4.1 mm long, 3.0–3.1 mm wide. Pericarp consisting of four layers: 1) locule lining five- to 12-seriate, composed of isodiametric to periclinally and horizontally elongate cells 10–15 μm thick and up to 33 μm long, 2) a uniseriate layer of columnar cells 55 to 140, avg. 80 μm high and 15–23 μm wide, 3) a 50 μm-thick layer of horizontally oriented narrow fibers each about 2.5–3.8 μm thick; layers 1–3 defining three pyrenes, which together are surrounded by 4) a layer of parenchyma cells 30–58 μm in diameter, 0.7–2.0 mm thick. Embryo circular in cross section, tube-like, aligned with the center of each locule.

Specimens.—Holotype: UF 9472. Paratypes: UF 9480, USNM 354051.

Discussion.—*Triplascapha* is represented by rare locule casts and permineralized fruits. The fruits are distinctive in the presence of a circular disk-like truncation at one end, possibly the apex (Pl. 63, figs. 1, 2, 7, 8), and the three dorsally concave locules that are symmetrically arranged about the long axis of the fruit (Pl. 63, fig. 10; Text-fig. 24). Typically, the outer layers of the fruit are stripped away as they are broken from the sediment, but one specimen still attached to the sedimentary matrix was sectioned to show the full thickness of mesocarp (Pl. 63, fig. 9). In size and form of the endocarp and locules, this fruit converges closely with *Portnallia* Reid et Chandler, a genus from the London Clay that has been synomized within the mastixioid genus *Beckettia* (Knobloch and Mai, 1986). For a detailed anatomical comparison, I was permitted to cut a transverse section of *Portnallia bognorensis* (v.30422, a specimen originally figured by Reid and Chandler, 1933, pl. 26, fig. 41). This section reveals that the London Clay endocarp is composed of swirling tracts of fibers, and lacks a central vascular bundle—characters that corroborate its assignment to the mastixioids and differentiate it from *Triplascapha.*

Transverse sections of *Triplascapha* reveal a distinctive columnar layer surrounding each of the three locules (Pl. 63, figs. 11, 12) that is not seen in extant or fossil mastixoids. The fibrous layer surrounding the columnar cell layer around each locule appears to define a pyrene, so that the three endocarps might have been shed independently unlike the situation in Cornaceae. The cylindrical, tube-like embryo (Pl. 63, figs. 10, 11) is a peculiarity that may eventually help in pinning down affinities with a particular modern family.

Genus TRIPLEXIVALVA gen. nov.

Etymology.—*Triplex* (L = threefold) + *valva* (L = door), referring to the three valves of the fruit.

Type species.—*Triplexivalva rugata* sp. nov.

Triplexivalva rugata sp. nov.

Plate 63, figures 13–20

Etymology.—*Rugosus* (L = wrinkled).

Description.—Fruit subglobose, nearly circular to rounded-triangular in cross section, rounded basally and apically, with a circular scar at the base, and a triangular to circular scar at apex; length 3.3–8.1, avg. 5.3 mm (SD=1.37, n=11), width 3.5–7.7, avg. 5.3 mm (SD=1.44, n=10), narrower width 2.8–7.5, avg. 4.8 mm (SD=1.83, n=6); composed of three well-defined valves, whose margins meet to form three longitudinal ridges that intersect apically and basally; asymmetrical, often with one valve somewhat larger than the others, valves up to 0.8 mm thick; surface longitudinally rugulate, rugulae thinning apically. Locule casts trigonal in transverse view, with the three carpels radially fused, sometimes with a cleavage between them, otherwise with a flange indicating the edges of adjoining valves.

Specimens.—Holotype: USNM 424799. Paratypes: UF 5237 (Bones, 1979, pl. 5, fig. 9), 6378–6380, 6382, 9725–9727, USNM 312759 (Bones, 1979, pl. 5, fig. 4), 355539 (2 specimens), 422396, 424798.

Discussion.—This species is represented by trigonal, globose fruit casts with prominent longitudinal ribs (Pl. 63, figs. 13–20). Circular spots on the surface of some specimens (Pl. 63, figs. 13, 15) might represent an exudate. Some of the specimens have shed one or more valves, showing that the valves themselves are relatively thick, and revealing a smooth locule cast inside (Pl. 63, figs. 17–20).

TRISEPTICARPIUM gen. nov.

Etymology.—Tri (L, Gr = three) + *septum* (L = partition) + *karpos* (Gr = fruit).

Type species.—*Trisepticarpium minutum* sp. nov.

Trisepticarpium minutum sp. nov.
Plate 64, figures 1–10

Etymology.—The epithet refers to the small size of the fruit.

Description.—Fruit pyriform, circular in cross section, base cuneate, rounded, apex hemispherical, rounded; length 2.8 mm, width 2.2 mm, tricarpellate, trilocular; surface smooth or faintly striate longitudinally, with three longitudinal grooves intersecting at the apex; outer wall of fruit 140 μm thick, composed of densely packed more or less isodiametric sclereids 25–50 μm in diameter, ventral wall of each carpel thicker than the outer fruit wall and comprised of a uni- to biseriate layer of large anticlinally elongate columnar cells 180–400 μm high, 40–100 μm wide; inner, ventral, wall of each carpel joining with those of adjacent carpels to form a prominent triradiate to triangular septum, locule lining composed of a uniseriate layer of horizontally oriented fibers 50 μm thick; locules dorsiventrally compressed 259–300 μm thick and 1150–1250 μm wide, containing small winged seeds, placentation axile and near the apex, seeds in cross section with a lensoidal central body 220–280 μm wide, 80 μm thick covered by a finely reticulate layer which is drawn out into a thin wing on both sides, width including wings 450 μm, wing width approximately as long as the width of the central body, straight or recurved near the margins, seeds arranged in two rows per locule, apparently with central placentation.

Specimen.—Holotype: USNM 424737.

Discussion.—This new genus and species is represented by a single well-preserved specimen which was photographed in stereo (Pl. 64, figs. 2, 3) and then sectioned transversely to reveal well preserved anatomy. The thick inner septa of this fruit, joined in a Y configuration (Pl. 64, figs. 5–9), and the winged seeds (Pl. 64, fig. 10), are distinctive features of this fruit.

Genus **TRUNCATISEMEN** gen. nov.

Etymology.—*Truncus* (L = cut off) + *semen* (L = seed).

Type species.—*Truncatisemen sapotoides* sp. nov.

Truncatisemen sapotoides sp. nov.
Plate 64, figures 11–14

Etymology.—The epithet refers to the similarity with seeds of Sapotaceae.

Description.—Seed ellipsoidal, bilaterally symmetrical, laterally compressed in the plane of symmetry with an oblique apical truncation, base and lateral margins smooth and rounded, length 9.5–12.2 mm, width in plane of symmetry 6.2–8.0 mm, thickness across plane of symmetry 5.5 mm; surface smooth, shiny, truncate face elliptical, 2.7–3.0 mm wide, 5.2–5.8 mm long, forming a slope about 35–40° to the long axis of seed, with a circular scar (hilum) in the center.

Specimens.—Holotype: UF 6459. Paratype: USNM 424650.

Discussion.—Both specimens of this species are preserved as chalcedony casts. Cracks on the surface of both fossil seeds suggest a thin, easily fractured seed coat. Similar obliquely truncate seeds occur in Styracaceae, Illiciaceae and Sapotaceae, however the precise familial affinities remain undetermined. Although there is a gross resemblance to seeds of some Sapotaceae, *Truncatisemen* does not show the characteristic bulging scar beneath the truncation that is typical of Sapotaceae. *T. sapotoides* differs from the Clarno truncate seeds attributed to *Bumelia?* by larger size, and lateral compression.

Genus **ULOSPERMUM** gen. nov.

Etymology.—*Ulo* (Gr = scar) + *spermum* (Gr = seed), referring to the prominent attachment scar.

Type species.—*Ulospermum hardingae* sp. nov.

Ulospermum hardingae sp. nov.
Plate 65, figures 1–8

Etymology.—This species is named after Elisabeth Harding, who collected one of the best specimens.

Description.—Fruit bilaterally symmetrical, obliquely cordiform in the plane of symmetry, with a large concave, elliptical scar at the broad end, pointed at the opposite end, oblong in cross section; fruit length 13.2–14.3, avg. 13.9 mm (SD=0.61, n=3), width 16.4–18.0, avg. 17.0 mm (SD=0.87, n=3), thickness across plane of symmetry 8.8–11.0, avg. 9.6 mm (SD=1.17, n=3), length/width ratio 0.73–0.87, avg. 0.82; the elliptical scar 6 × 9 mm, containing many (about 20) protruding V- or Y-shaped vascular traces; wall 0.8 mm thick, made up of three anatomical layers: 1) uni- to biseriate locule lining ca. 30 μm thick composed of thin walled poorly preserved periclinally elongate rectangular cells 12–15 μm in diameter, 2) a middle layer ca. 250 μm thick composed of anticlinally organized files of densely packed small sclereids 12–22 μm wide, 30–38 μm long, grading into, 3) outer layer composed of larger cells 40–80 (–130) μm in diameter that are not anticlinally aligned, grading from more or less isodiametric to larger and periclinally elongate toward the periphery. Locule cast relatively smooth, in one specimen bearing small, evenly spaced punctae.

Specimens.—Holotype: USNM 355363. Paratypes: UF 9566, USNM 414509, 355363.

Discussion.—This species is rare in the Nut Beds collections and is unknown from other localities. Two of the specimens are locule casts with the outer wall missing (e.g., Pl. 65, figs. 1–3). The tissue over the large recessed scar appears to have been well-indurated, and has remained intact in one specimen (Pl. 65, fig. 1), but when removed, shows numerous vascular bundle endings (Pl. 65, figs. 2–4). The holotype has the wall intact, permineralized, and, upon sectioning, yielded the anatomical details described above (Pl. 65, figs. 5–8). Although *Ulospermum* could be interpreted either as a seed with a conspicuous hilum, or as a fruit with a conspicuous cupule or pedicel scar, I have described it as a fruit, because the specimen that was cut transversely shows the remains of what appears to be a seed shriveled in the center of the locule (Pl. 65, fig. 5). Despite the very distinctive morphology, I have been unable to determine its affinity among extant families.

Genus **WHEELERA** gen. nov.

Etymology.—This genus is named for Elisabeth A. Wheeler, recognizing her contributions to paleobotany including research on woods of the Clarno flora.

Type species.—*Wheelera lignicrusta* sp. nov.

Wheelera lignicrusta sp. nov.
Plate 65, figures 9–16

Etymology.—*Lignum* (L = wood) + *crusta* (L = shell), referring to the fibrous fruit wall.

Description.—Fruit subglobose, prolate, rounded basally and apically, unilocular, length 11.4–12.0 mm, equatorial diameter 8.0–8.4 mm; pericarp 1.4–2.0 mm thick, composed of: 1) uniseriate locule lining of thick-walled anticlinally oriented columnar cells 100 μm high, 25 μm wide that commonly contain one to four rhomboidal crystals, 2) a thick layer of short fibers 300–600 μm long, 40–70 μm wide, 3) an outer layer about 200 μm thick composed of tangentially flattened of parenchyma cells 60–100 μm wide, 13–40 μm high. Locule cast smooth, rounded basally, pointed apically.

Specimens.—Holotype: UF 9271. Paratypes: UF 9576, 9359.

Discussion.—This species is known from three permineralized specimens. The main thickness of the pericarp formed of anticlinally directed short fibers (Pl. 65, fig. 15), and the locule lining of columnar cells with crystals (Pl. 65, fig. 16) are distinctive features of this genus. As yet, the affinities with modern taxa remain undetermined.

Genus **CARPOLITHUS** Schlotheim

Carpolithus bellispermus Chandler
Plate 66, figures 1–10

Carpolithus bellispermus Chandler 1978, pp. 31–32, pl. 8, figs. 3–6.

Description.—Seed ovate in face view, dorsiventrally compressed, rounded-triangular in cross section, typically bilaterally symmetrical except at the laterally oblique apex; base rounded, apex in complete seeds rounded, slightly bulging, with an asymmetrical, angular notch visible on the dorsal and ventral surfaces; dorsal side of seed gently convex, ventral side typically with two faces meeting at about 120° to form a rounded median longitudinal ridge; length of complete seed 2.8–3.2, avg. 3.0 mm (SD=0.19, n=7), width 1.5–2.0, avg. 1.8 mm (SD=0.17, n=7), thickness 0.9–1.1, avg. 1.0, (SD=0.08, n=7); seed coat composed of two cell layers: inner layer uniseriate, about 0.02 mm thick, composed of small, rectangular to polygonal cells more or less longitudinally aligned as viewed peridermally; outer layer 0.125 mm thick, uniseriate with large cells that are adjoining basally, but with each cell narrowed apically and forming a cylindrical digitate projection, digitations about 30 μm in diameter, oriented anticlinally, resulting in a papillate surface to the seed coat; digitations are encased in a tan to brownish translucent substance, possibly wax, that forms the outer surface of the seed. Endosperm cast (internal mold of seed coat) shaped like the complete seeds, except obliquely truncate apically, the plane of truncation oriented 45–60° to the longitudinal axis as viewed ventrally or dorsally; micropyle forming a prominent point at the top of the apical truncation.

Specimens.—UCMP 10663–10667, 10698–10700; USNM 355416, 435014–435017; UF 6503–6506, 8544–8579, casts; UCMP 10696, 10697, UF 6607, specimens with intact seed coat. Holotype: BM v51663 (London Clay).

Discussion.—*Carpolithus bellispermus* was recognized previously only from the Eocene Bognor Beetle Bed of the London Clay, England (Chandler, 1978). The familial affinities are still unknown, and the species is retained provisionally in the noncommittal genus *Carpolithus*. It is represented in the Nut Beds by numerous internal chalcedony molds of seed coat, and a few permineralized specimens with the seed coat intact. The internal molds are readily recognized by the smaller size, obliquely truncate apex, rounded base, dorsiventral compression and median ventral ridge (Pl. 66, figs. 5, 6). Complete seeds show the notched apex (Pl. 66, figs. 1–4) and digitate outer layer (Pl. 66, figs. 7–9). The closely spaced, anticlinally oriented digitate cells, enveloped in a translucent layer, are conspicuous features that should be helpful in the search for related extant and/or fossil taxa. Despite good preservation of the seed coat in some of the specimens, no embryo and no raphe were observed.

In the description above I have followed Chandler's (1978) interpretation that these specimens represent seeds rather than fruits. Chandler (1978) provided a brief description of fruit characters based upon specimen(s) that she had observed prior to pyritic deterioration. She stated that only part of the endocarp was preserved, bearing a single seed and having a longitudinal suture with rounded edges along which splitting had occurred and noted that the was wall columnar in section. She interpreted the seeds to be campylotropous because of the adjacent hilum and micropyle without an obvious raphe. Corresponding fruits have not been recovered from the Nut Beds, but the seeds are so distinctive that there can be no question in identifying this material to the London Clay species.

Carpolithus sp. 1
Plate 66, figures 11–14

Description.—Endocarp unilocular, ellipsoidal, nearly circular in cross section, 7.8–11.0 mm long, 6.1–6.9 mm in diameter, base and apex rounded, surface longitudinally ribbed, with about eight to ten prominent, rounded meridional ridges, each with a groove at its crest; endocarp wall 0.7 mm thick.

Specimens.—USNM 355686, OMSI Pb1439.

Discussion.—This eight- to ten-ribbed fruit is represented by two specimens from the lower part of Face 3. Neither is anatomically preserved, but the external morphology indicates that it represents a species distinct from any other known from the Nut Beds.

Carpolithus sp. 2
Plate 66, figures 15, 16

Description.—Achene bisymmetrical, ovate in lateral view, base truncate, apex acute; laterally compressed in the plane of symmetry with a wing-like keel on one side, rounded on the other side; length 2.4–2.7 mm, width 1.6–1.7 mm, thickness 1.0–1.1 mm; truncate base with an elliptical recessed area (hilum or pedicel scar), surface smooth on the rounded margin, but cratered with shallow depressions up to 200 μm in diameter on the lateral margins and on the wing-like portion.

Specimens.—USNM 424719, UF 8581.

Discussion.—This species is represented by hollow silica casts that appear to represent achenes. Distinctive features are the relatively large circular basal scar (Pl. 66, fig. 16), the cratered surface and wing-like keel on one side.

Carpolithus sp. 3
Plate 66, figures 17, 18

Description.—Seed prolate, ellipsoidal, circular-elliptical in cross section, base and apex rounded, elliptical in cross section, length 6.4 mm, diameter at equator 5.0 × 5.8 mm, surface smooth; seed coat 280 μm thick, composed of: 1) an inner layer ca. 200 μm thick of more or less isodiametric parenchyma cells 13–30 μm in diameter, 2) a middle layer ca. 50 μm thick of tangentially flattened sclerenchyma, 3) an outer layer about 40 μm thick composed of larger thin-walled angular parenchyma cells 30–50 μm in diameter. Cotyledons large, plano-convex, hemispherical.

Specimen.—USNM 355069.

Discussion.—This species is represented by a single specimen. Although the outer surface is rather nondescript, sectioning revealed a thick wall and large planoconvex cotyledons (Pl. 66, fig. 18). Although similar to Lauraceae in the single locule and large hemispherical cotyledons, the columnar layers typical of that family were not observed. The preserved wall is interpreted above as representing the seed coat, but it may also include part of the fruit wall.

Carpolithus sp. 4
Plate 67, figures 1–5

Description.—Locule cast obpyriform, bisymmetrical, nearly circular in cross section, but with a raised longitudinal ridge in the plane of symmetry, base and apex pointed, widest about ⅓ of the distance below apex, length 5.0 mm, diameter 2.0 mm; the longitudinal ridge formed only on one side in the plane of symmetry, appearing as a flattened band 0.7 mm wide with a median keel; single-seeded with thin seed coat preserved.

Specimen.—USNM 424652.

Discussion.—This specimen appears to be the locule cast of a unilocular fruit. The longitudinal ridge, which is only on one side (ventral?) apparently represents the suture plane (Pl. 67, figs. 1–4). A transverse section reveals a single seed inside with a thin seed coat preserved (Pl. 67, fig. 5). At least superficially, it resembles the locule of *Prunus* (Mai, pers. comm., 1989), but it does not correspond to the locule morphology of either of the *Prunus* species known from permineralized endocarps from the Nut Beds.

Carpolithus sp. 5
Plate 67, figures 6–8

Description.—Fruit unilocular, single-seeded, endocarp more or less ellipsoidal, elliptical in cross section, length 3.4 mm, width 3.1 mm, thickness 2.0 mm; endocarp wall smooth, 230–330 μm thick, ca. 12-seriate, composed of rounded cells with small extensions, adjacent cells adjoining like pieces of a jig-saw puzzle, these cells typically 15–40 μm in diameter; exocarp uniseriate with inflated, thin-walled rectangular cells, 25–58 μm wide, 20–38 μm high, and an outer biseriate layer of square to rectangular cells 10–13 μm in diameter. Seed coat uniseriate, composed of cuboidal cells about 10 μm in diameter.

Specimen.—UF 9758.

Discussion.—This species is represented by a single well-preserved specimen. It was sectioned transversely revealing the pericarp thickness and a single seed with a shriveled thin seed coat (Pl. 67, figs. 6, 7). The endocarp composed of interdigitating rounded cells, and exocarp of thin-walled rectangular cells are distinctive features of this species (Pl. 67, fig. 8). The unilocular, single-seeded morphology and interconnecting cells of the endocarp are reminiscent of Icacinaceae; however, the endocarp shows no obvious plane of dehiscence as occurs in many Icacinaceae and a funicular canal was not detected. The affinities of this species, whether within the Icacinaceae, or with another family, remain to be determined.

Carpolithus sp. 6

Plate 67, figures 9–12

Description.—Fruit subovoid, unilocular, single-seeded, base and apex rounded, length 5.1 mm, width 4.2 mm, thickness 3.9 mm; endocarp ellipsoidal, bisymmetrical, laterally compressed with a keel in the plane of symmetry, endocarp wall 0.2 mm thick, with smooth locule and verrucate outer surface, composed of thick-walled sclereids 20–38 μm in diameter; mesocarp 0.6–0.9 mm thick, composed of large, polygonal, isodiametric to anticlinally elongate parenchyma cells 80–160 μm in diameter, these cells smaller in the outer few peripheral layers and with about 30 longitudinally oriented vascular bundles close to the endocarp; large empty cavities developed in parts of the mesocarp; placentation ventral near the base; seed filling the locule, seed coat composed of two to three layers of rectangular, periclinally elongate cells; raphe with several vascular bundles forming a band 400 μm thick and 100 μm wide along one of the lateral margins adjacent to the keel of the endocarp.

Specimen.—USNM 424738.

Discussion.—This species is known from a single specimen that is not very distinctive in its surface morphology (Pl. 67, figs. 9, 10), but in section shows good anatomical structure (Pl. 67, figs. 11, 12). The mesocarp appears to have been rather soft, and one would expect the endocarp alone to be more commonly preserved. However, I have not seen corresponding isolated endocarps with the distinctive verrucate surface ornamentation observed in this species.

Carpolithus sp. 7

Plate 67, figures 13–16

Description.—Locule cast subglobose-oblate, rounded basally, truncate apically, height 7.5, 11, 12.1 mm, equatorial diameter 8.5, 13.8, 14.1 mm; surface smooth to irregularly wrinkled; truncation smooth, more or less circular, perpendicular to the vertical axis, its margins somewhat recessed, slightly domed (wide-obtusely conical) forming an obtuse point in the center. Mold in matrix globose, with very little space between cast and mold, at most 0.2 mm, with a small domed projection at one end.

Specimens.—UF 9862, USNM 355191, 355637.

Discussion.—This species is distinctive in its globose shape and circular, shallowly domed truncation. One of the specimens (UF 9862) is a cast along with a mold of the surrounding endocarp. The space between the locule cast and the endocarp mold, representing the endocarp wall thickness, is only about 0.2 mm. Such a thin wall may explain the surface wrinkling, which could be due to compaction in the sediment.

Carpolithus sp. 8

Plate 68, figures 1–4

Description.—Achene more or less ovoid, truncate at one end, rounded-acute at the other; more or less circular in cross section, length 4.0 mm, equatorial diameter 3.4 mm, exterior smooth, base with a recessed circular scar, wall relatively thick (0.8 mm), composed of isodiametric cells 23–63 μm in diameter; locule lining composed of a single layer of small cuboidal cells ca. 7 μm in diameter.

Specimen.—USNM 422526.

Discussion.—This species is known from a single specimen that is distinctive in its thick wall and large basal scar. Preliminary study indicates close similarity in morphology and anatomy to extant *Sparganium*. *Sparganium* achenes are truncate at the apex, and, like those of the fossils, have an endocarp of a single relatively thick layer of isodiametric cells.

Carpolithus sp. 9

Plate 68, figures 5–9

Description.—Fruit or bud subglobose, trigonal in cross section, pointed at one end, truncate at the other, with three longitudinal keels intersecting at the pointed end; length 2.0–2.5 mm, width 1.6–2.4 mm; truncate end with a central circular scar (style base or peduncle scar?) surrounded by four alternately arranged whorls of three slits interpreted as tepal scars; wall (endocarp?) 200 μm thick.

Specimens.—UF 6347, 6457, 9550–9556.

Discussion.—These specimens are distinctive in their trigonal symmetry and truncated end with whorls of slits that appear to represent tepals. Whether these objects represent immature buds or actual fruits has not been determined. Transverse sections failed to reveal stamens, as might be expected if the specimens represent flower buds. The sections also did not reveal seeds.

Carpolithus sp. 10
Plate 68, figures 10–14

Description.—Fruits/seeds trigonal in face view, bisymmetrical, with a dorsal keel in plane of symmetry, height 1.4–1.7, avg. 1.6 mm, (SD=0.13, n=4), width across plane of symmetry 0.9–1.1, avg. 1.0 mm (SD=0.08, n=4), depth in plane of symmetry 1.6–1.7, avg. 1.7 mm (SD=0.06, n=3); rounded dorsally, narrowly triangular in ventral view; with pore (hilum or funicular opening) circular on the ventral surface.

Specimens.—USNM 435102–435105.

Discussion.—This species is represented only by a few specimens. In shape and size they compare favorably with *Brousonettia* in the Moraceae. The species of *Brousonettia* that I have seen have a verrucate seed coat, whereas this fossil species has a smooth outer surface. Moraceous wood anatomically similar to *Brousonettia* is present among the fossil woods from the Nut Beds (Manchester, unpublished).

Carpolithus sp. 11
Plate 68, figures 15–19

Etymology.—The epithet refers to the Clarno Formation.

Description.—Inner mold of seed coat oblong in face view, bilaterally symmetrical; base rounded, apex apparently rounded, dorsiventrally compressed, somewhat curved ventrally from base to apex as seen from the side, length ca. 11.3 mm, width ca. 4.9 mm, thickness ca. 2.0 mm, with a median keel on the dorsal surface and broad median depression on the ventral side; surface of mold with about 22 closely spaced, rounded horizontal ribs arising oppositely from the median keel. These ribs are straight in course, passing from the dorsal keel over the dorsal face and around to the ventral side where the meet in an offset pattern, the ribs perpendicular to the long axis of the seed except at the base and apex where they are radially arranged.

Specimen.—USNM 424625.

Discussion.—This species is represented by a single very distinctive specimen showing a series of rounded transverse ridges separated by narrow cleavages (Pl. 68, figs. 15–19). The specimen is interpreted as the internal mold of a seed, suggesting that the seed coat itself had a series of transverse partial septa and that the endosperm was therefore ruminate. Unlike the seeds of Annonaceae with ruminate endosperm (Pl. 6, figs. 9–18), the species has a prominent dorsal keel, and the ribs are more parallel and even in their development. Ruminate endosperm also occurs among the Menispermaceae (Thanikaimoni, 1984), and in shape and symmetry the fossil resembles endocarps of the Tinosporeae tribe; however, I have not found a closely similar modern genus, and the apex of the fossil is broken, making it impossible to determine if placentation was subapical as in Tinosporeae.

Carpolithus sp. 12
Plate 69, figure 1–4

Description.—Fruit a penta-syncarpellate capsule, prolate, rounded in lateral view, with five locules radially arranged about a central axis; length 11.5 mm, width 8.3–10.1 mm; surface smooth, each carpel with a median longitudinal dorsal keel, possibly a line of dehiscence; adjacent carpels separated by a groove on the external surface and by a thin septum (ca. 0.4 mm) formed by the paired carpel walls; number and type of seeds unknown.

Specimen.—USNM 326719 (Bones, 1979, pl. 5, fig. 10).

Discussion.—This species is represented by a single specimen with five conspicuously bulging locules (Pl. 69, figs. 1–3). The fruit was sectioned transversely revealing thin septa, a thick central axis, and empty locules (Pl. 69, fig. 4) suggesting that the seeds had dispersed prior to deposition of the fruit.

Carpolithus sp. 13
Plate 69, figures 5–8

Description.—Fruit subglobose, unilocular, single-seeded?, rounded apically and basally; length and width 15.0 mm; surface smooth; wall 2.7 mm thick, composed of: locule lining 6–7-seriate, 600 μm thick, composed of anticlinally elongate cells 70–120 μm long, 20–45 μm wide; outside the locule lining is a uniseriate layer 20 μm thick of narrow anticlinally elongate cells, poorly preserved, frequently expanded and containing rhomboidal crystals; mesocarp not preserved, represented by a space 1.6 mm thick penetrated by foreign roots; exocarp composed of a layer of isodiametric sclereids 50–75 μm in diameter, outlined by a uniseriate layer 15 μm thick composed of rectangular cells 15–30 μm in diameter.

Specimen.—UF 9744.

Discussion.—This species is represented by a single specimen. Although the exterior of the specimen is fractured and partially covered with sediment (Pl. 69, fig. 5), the internal structure and anatomy is very well preserved as seen in transverse sections (Pl. 69, figs. 6–8). The inner layer of short, anticlinally elongate thin-walled cells (Pl. 69, fig. 7) and the outer layer of compact isodiametric sclereids (Pl. 69, figs. 8) are conspicuous features of this fruit.

Carpolithus sp. 14
Plate 69, figures 9–12

Description.—Fruit a multiseeded berry, pyriform, circular in cross section, pointed apically, rounded with a slight depression and 1 mm circular scar at the base; length 12.2 mm, equatorial diameter 11.3 mm; fruit surface smooth, evidently thin-walled; placentation type uncertain, seeds ovoid, 1.8–2.8 wide, ca. 5.0 mm long, borne in three pairs near the center of the fruit and surrounded by pulpy tissue; seed coat composed of a layer of uniseriate, anticlinally oriented columnar cells 50–70 μm high and 20–25 μm wide.

Specimen.—UM 66137.

Discussion.—This species is known only from a single specimen. Transverse sectioning showed that much of the inner contents had degraded prior to silicification; however, a central group of six paired seeds are recognizable, two of which are well preserved (Pl. 69, figs. 11, 12). Toward the periphery of the fruit are remains of what appear to be degraded parenchyma tissue suggesting that it was a fleshy fruit.

Carpolithus sp. 15
Plate 69, figures 13–16

Description.—Cast bisymmetrical, H-shaped in face view, consisting of two crescent shaped limbs, each more or less parallel, concave ventrally and convex dorsally, rounded at one end, narrowed and pointed at the other; these limbs mutually joined connected across the plane of symmetry in the central ⅓ of their length; height 5.7 mm, width across plane of symmetry 4.0 mm, thickness 3.5 mm; surface nearly smooth, but finely striate by surface cells oriented horizontally with respect to the long axis of each limb; dorsiventral thickness of each limb 2.2 mm, each limb with a dorsal keel that is best developed at the narrow end.

Specimen.—UF 9548.

Discussion.—Only a single specimen of this type is known. It is distinctive in the H-shape in face view (Pl. 69, figs. 13, 14) and strongly curved longitudinal axis as viewed laterally (Pl. 69, fig. 15). The structure apparently represents the inner mold of a seed (embryo cast) or fruit (locule cast). If it is an embryo cast then the two limbs might be interpreted as a pair of thick cotyledons. If it is a locule cast, then the fruit appears to have been almost bilocular, but with a foramen between the two lateral halves.

Carpolithus sp. 16
Plate 70, figures 1–5

Description.—Seed laterally flattened, ellipsoidal, bilaterally symmetrical with a ventral keel in plane of symmetry, rounded dorsally, length 3.2 mm, width 2.0 mm, thickness 1–1.2 mm; surface with prominent narrow rugulations perpendicular to long axis of seed. Embryo cavity smooth-surfaced, laterally compressed like the seed, roughly J-shaped with notch in the placental area.

Specimens.—UF 9609, 9794–9798.

Discussion.—Seeds of this species are preserved together in clusters within the siltstone. Typically the seed coat itself has deteriorated, leaving a rugulate outer mold in the siltstone with a silica cast of the embryo cavity inside. The surficial relief on the seeds can be seen through stereo images of the matrix mold (Pl. 70, figs. 1, 2), and on silicone casts prepared from the same specimens (Pl. 70, fig. 5). Although internal composition of the seed is unknown, internal molds of the seed coat (Pl. 70, figs. 3, 4) are curved, suggesting a curved embryo, with an attachment scar at the axis of curvature.

Carpolithus sp. 17
Plate 70, figures 6–8

Description.—Fruit globose-prolate, unilocular, single-seeded, base and apex rounded, circular in transverse section, length 6.2 mm, equatorial diameter 5.5 mm; pericarp 1.25 mm thick, consisting of a thick parenchymatous layer of isodiametric cells 30–70 μm in diameter surrounded by a uniseriate layer of anticlinally elongate schlerenchyma cells 210 μm high, 30–38 μm wide; seed coat 38 μm thick, four- to six-seriate, composed of thin walled polygonal cells 8–15 μm high, 12–30 μm, seed filled with parenchyma 50–180 μm in diameter.

Specimen.—UF 9768.

Discussion.—This globose unilocular specimen shows some similarity to the fruits of Lauraceae. However, although it has an outer layer of columnar cells, its lacks such a layer close to the locule and it does not show the large, subhemispherical cotyledons typical of Lauraceous seeds.

Carpolithus sp. 18
Plate 70, figures 9–12

Description.—Fruit broadly elliptical in face view, lenticular to compressed-hexagonal in cross section, unilocular, quadrilaterally symmetrical with the two planes of symmetry intersecting at right angles in the longitudinal axis), with a median keel in the dorsiventral plane of symmetry; ventral and dorsal faces rounded or with a pair of longitudinal angles, base rounded-truncate with a persistent stalk 0.7 mm long and 0.4 mm thick, apex rounded; fruit length 6.8 mm, width 6.2 mm, thickness 4.7 mm; wall 123–150 μm thick, seed similar in shape to the fruit, raphe running longitudinally down one of the narrow sides.

Specimens.—UF 6497, 9464.

Discussion.—This species is represented only by two specimens, one of which is fragmentary. One of them was sectioned transversely, revealing a thin wall and large locule devoid of contents (Pl. 70, fig. 12). In the cutting process, the wall flaked away on the apical half, revealing an internal cast of the seed showing the course of the raphe on one side along the keel. The description above uses terminology that assumes the specimen is a fruit containing a single seed. Alternatively, the specimen might be interpreted as a seed with the outer wall representing the seed coat and the projection a prominent protruding hilum. The other specimen shows some poorly preserved dark organic material adhering to the fruit cast, indicating that the specimens are missing the outer layer(s).

Carpolithus sp. 19

Plate 70, figures 13, 14

Description.—Cast globose, rounded apically and basally, length 15.2 mm, equatorial diameter 15.6 mm; apical ⅓ with three equidistant faint longitudinal ridges joining at the apex to form a triradiate mark; surface smooth in the lower hemisphere, striate in the upper hemisphere with longitudinally aligned low rounded ribs that are intertwining and plicate at their extremities.

Specimen.—USNM 422381.

Discussion.—This specimen is a cast in translucent chalcedony without cellular preservation. It appears to be the internal mold of a fibrous endocarp or seed coat. Because of the triradiate mark at the apex (Pl. 70, figs. 13, 14), it brings to mind Palmae. There is no evidence, however, of germination openings.

Carpolithus sp. 20

Plate 70, figures 15, 16

Description.—Fruit globose, unilocular, single-seeded, rounded apically and basally, length 7.5 mm, width 6.5 mm; wall 0.9 mm thick, composed of isodiametric sclereids 38–63 μm in diameter.

Specimens.—UF 9759, 9760.

Discussion.—This species is represented by two specimens. The layer of isodiametric sclereids composing the fruit wall distinguishes it from other unilocular fruits of the Nut Beds. Although similar in size and shape to *Prunus weinsteinii*, this species does not show a keel or plane of dehiscence.

Carpolithus sp. 21

Plate 70, figure 18

Description.—Seed cordate, quadrilaterally symmetrical, length 6.5 mm, width 8 mm, thickness 3.8 mm (est.); internal mold of seed coat more or less triangular in face view, dorsiventrally compressed, fusiform in transverse section, smooth to faintly rugulate, 5.8 mm long, 5.7 mm wide, 1.9 mm thick, rounded basally, with a protruding scar of attachment, pointed apically; seed coat thickness 1.2 mm.

Specimen.—USNM 422525.

Discussion.—This species is known only from a single specimen. Although it bears some resemblance to seeds of Magnoliaceae, it is perfectly symmetrical. The inner cast is smooth, however the surrounding mold in the sediment is rough-textured with protrusions (Pl. 70, fig. 18).

Five-part flower

Plate 70, figure 17

Description.—Flower 5-parted, actinomorphic, ca. 18 mm wide, with central circular structure (ovary?) 4.5 mm in diameter, five free ovate sepals 7.0 mm long, 3–5 mm wide, five free petals alternate with and thinner than the sepals, with pronounced parallel veins. Pedicel 1.2 mm in diameter, at least 3 mm long.

Specimens.—OMSI Pb1507, 1642.

Discussion.—Two flowers of this type were recovered from the leaf stratum at the base of Face 3. One is transversely compressed (Pl. 70, fig. 17), the other is laterally compressed.

REFERENCES CITED

Airy Shaw, H. K., ed.
1973. *A dictionary of the flowering plants and ferns.* 8th ed. Cambridge University Press, Cambridge, England, 1245 pp.

Axelrod, D. I., Arroyo, M. T., and Raven, P. H.
1991. *Historical development of temperate vegetation in the Americas.* Revisita Chilena de Historia Natural, vol. 64, pp. 413–446.

Bailey, I. W. and Howard, R. A.
1941. *The comparative morphology of the Icacinaceae I. Anatomy of the node and internode.* Journal of the Arnold Arboretum, vol. 22, pp. 125–132.

Basinger, J. F.
1981. *The vegetative body of* Metasequoia milleri *from the Middle Eocene of southern British Columbia.* Canadian Journal of Botany, vol. 59, pp. 2379–2410.

Basinger, J. F. and Rothwell, G. W.
1977. *Anatomically preserved plants from the Middle Eocene (Allenby Formation) of British Columbia.* Canadian Journal of Botany, vol. 55, pp. 1984–1990.

Becker, H. F.
1969. *Fossil plants of the Tertiary Beaverhead Basins in southwestern Montana.* Palaeontographica, Abt. B, vol. 127, pp. 1–142, pl. 1–44.

Berry, E. W.
1930. *Revision of the Lower Eocene Wilcox flora of the southeastern United States.* U.S. Geological Survey Professional Paper 156, pp. 1–196.

Bestland, E. A., Retallack, G. J., Swisher, C. C., and Fremd, T. J.
1993. *Timing of cut-and-fill sequences in the John Day Formation (Eocene-Oligocene), Painted Hills Area, Central*

Oregon. Geological Society of America, Abstracts with Programs, vol. 25, no. 5, p. 9.

Beusekom, C. F. van

1971. *Revision of* Meliosma *(Sabiaceae), section* Lorenzanea *excepted, living and fossil, geography and phylogeny.* Blumea, vol. 19, pp. 355–529.

Blanc-Louvel, C.

1985. *Paléoflore du Gisement Éocène de Prémontré dans L'Aisne: Étude de deux fruits.* 110ᵉ Congrès national des Sociétés savantes, Montpellier, 1985, sciences, fasc. 5, pp. 149–161, pl. 1–3.

Bogle, A. L. and Philbrick, C. T.

1980. *A generic atlas of hamamelidaceous pollens.* Contributions of the Gray Herbarium, vol. 210, pp. 29–103.

Bones, T. J.

1979. *Atlas of fossil fruits and seeds from North Central Oregon.* Oregon Museum of Science and Industry Occasional Papers in Natural Science, vol. 1, pp. 3–23.

Bremekamp, C. E. B.

1966. *Remarks on the position, the delimitation and the subdivision of the Rubiaceae.* Acta Botanica Neerlandica, vol. 15, pp. 1–33.

Bremer, B. and Struwe, L.

1992. *Phylogeny of the Rubiaceae and the Loganiaceae: Congruence or conflict between morphological and molecular data.* American Journal of Botany, vol. 79, pp. 1171–1184.

Brown, J. T.

1975. Equisetum clarnoi, *a new species based on petrifactions from the Eocene of Oregon.* American Journal of Botany, vol. 62, pp. 410–415.

Brown, R. W.

1929. *Additions to the flora of the Green River Formation.* U.S. Geological Survey Professional Paper 154-J, pp. 279–293, 7 pl.

1940. *New species and changes of name in some American fossil floras.* Journal of the Washington Academy of Sciences, vol. 30, pp. 344–353.

Camus, A.

1952–1954. *Les chênes.* in Encylopédie Économique de Sylviculture, vol. 8, pp. 511–1196.

Cevallos-Ferriz, S. R. S. and Stockey, R. A.

1988a. *Permineralized fruits and seeds from the Princeton chert (Middle Eocene) of British Columbia: Lythraceae.* Canadian Journal of Botany, vol. 66, pp. 303–312.

1988b. *Permineralized fruits and seeds from the Princeton chert (Middle Eocene of British Columbia: Araceae.* American Journal of Botany, vol. 75, pp. 1099–1113.

1989. *Permineralized fruits and seeds from the Princeton chert (Middle Eocene) of British Columbia: Nymphaeaceae.* Botanical Gazette, vol. 150, pp. 207–217.

1990. *Permineralized fruits and seeds from the Princeton chert (Middle Eocene) of British Columbia: Vitaceae.* Canadian Journal of Botany, vol. 68, pp. 288–295.

1991. *Fruits and seeds from the Princeton chert (Middle Eocene) of British Columbia: Rosaceae (Prunoideae).* Botanical Gazette, vol. 152, pp. 369–379.

Chandler, M. E. J.

1926. *The Upper Eocene flora of Hordle, Hants.* The Palaeontographical Society, London, 52 pp., 8 pl.

1957. *The Oligocene flora of the Bovey Tracey Lake Basin, Devonshire.* Bulletin of the British Museum (Natural History) Geology, vol. 3, pp. 71–123, pl. 11–17.

1960. *Plant remains of Hengistbury and Barton Beds.* Bulletin of the British Museum (Natural History) Geology, vol. 4, pp. 193–238, pl. 29–35.

1961a. *Flora of the Lower Headon Beds of Hampshire and the Isle of Wight.* Bulletin of the British Museum (Natural History) Geology, vol. 5, pp. 91–158, pl. 24–30.

1961b. *The Lower Tertiary floras of southern England. 1. Paleocene Floras. London Clay Flora (Supplement). Text and Atlas.* British Museum (Natural History), London, xi + 354 pp., 34 pl.

1962. *The Lower Tertiary floras of southern England. 2. Flora of the Pipe-Clay Series of Dorset (Lower Bagshot).* British Museum (Natural History), London, xi + 176 pp., 29 pl.

1963a. *Revision of the Oligocene floras of the Isle of Wight.* Bulletin of the British Museum (Natural History) Geology, vol. 6, pp. 321–384, pl. 27–35.

1963b. *The Lower Tertiary floras of southern England. 3. Flora of the Bournemouth Beds; the Boscombe, and the Highcliff Sands.* British Museum (Natural History), London, xi + 169 pp., 25 pl.

1964. *The lower Tertiary floras of southern England. 4. Summary and survey of findings in the light of recent botanical observations.* British Museum (Natural History), London, xii + 151 pp., 4 pl.

1978. *Supplement to the Lower Tertiary Floras of Southern England.* Tertiary Research Special Paper, vol. 4, pp. 1–44.

Chaney, R. W.

1927. *Geology and Palaeontology of the Crooked River Basin, with special reference to the Bridge Creek flora.* Carnegie Institute of Washington Publication 346, pp. 45–138, pl. 2–20.

Cheesman, E. E.

1947. *Classification of the bananas. I The genus* Ensete *Horan.* Kew Bulletin, vol. 2, pp. 97–117.

Chernik, V. V.

1980. *Peculiarities of structure and development of the pericarp of the representatives of the family Ulmaceae and Celtidaceae.* Botanicheskii Zhurnal, vol. 65, pp. 521–531 (In Russian).

Collinson, M. E.

1982. *A preliminary report on the Senckenberg-Museum collection of fruits and seeds from Messel bei Darmstadt.* Courier Forschungsinstitut Senckenberg, vol. 56, pp. 49–57.

1983. *Fossil plants of the London Clay.* The Palaeontological Association, London, England, 121 pp.

1988. *The special significance of the Middle Eocene fruit and seed flora from Messel, Western Germany.* Courier Forschungsinstitut Senckenberg, vol. 107, pp. 187–197.

Collinson, M. E. and Hooker, J. J.

1987. *Vegetational and mammalian faunal changes in the Early Tertiary of southern England,* in Friis, E. M., Chaloner, W. G., and Crane, P. R. [eds.], *The origins of angiosperms and their biological consequences*, pp. 259–304. Cambridge University Press, Cambridge, England.

1992. *Fossil evidence of interactions between plants and plant-eating mammals.* Philosophical Transactions of the Royal Society, London, B, vol. 333, pp. 197–208.

Corner, E. J. H.

1976. *The seeds of dicotyledons.* Cambridge University Press, Cambridge, England, 2 vol., 311 + 552 pp.

Cowan, D. S.

1982. *Geological evidence for a post-40 m.y. B.P. large-scale displacement of part of southeastern Alaska.* Geology, vol. 10, pp. 309–313.

Crane, P. R.

1981. *Betulaceous leaves and fruits from the British Upper Palaeocene*. Botanical Journal of the Linnean Society, vol. 83, pp. 103–136.

1987. *Vegetational consequences of the angiosperm diversification*, in Friis, E. M., Chaloner, W. G., and Crane, P. R. [eds.], *The origins of angiosperms and their biological consequences*. pp. 107–144, Cambridge University Press, Cambridge, England.

1989. *Early fossil history and evolution of the Betulaceae*, in Crane, P. R. and Blackmore, S. [eds.], *Evolution, Systematics, and fossil history of the Hamamelidae*, Volume 2: 'Higher' Hamamelidae. Systematics Association Special Volume no. 40B, pp. 87–116, Clarendon Press, Oxford, England.

Crane, P. R., Manchester, S. R., and Dilcher, D. L.

1990. *A preliminary survey of fossil leaves and well-preserved reprod structures from the Sentinel Butte Formation (Paleocene) near Almont, North Dakota*. Fieldiana Geology, New Series, no. 20, pp. 1–63.

Crepet, W. L.

1989. *History and implications of the early North American record of Fagaceae*, in Crane, P. R. and Blackmore, S. [eds.]. *Evolution, Systematics, and fossil history of the Hamamelidae*, Volume 2: 'Higher' Hamamelidae. Systematics Association Special Volume no. 40B, pp. 45–66, Clarendon Press, Oxford, England.

Crepet, W. L. and Nixon, K. C.

1989a. *Earliest megafossil evidence of Fagaceae: phylogenetic and biogeographic implications*. American Journal of Botany, vol. 76, pp. 842–855.

1989b. *Extinct transitional Fagaceae from the Oligocene and their phylogenetic implications*. American Journal of Botany, vol. 76, pp. 1493–1505.

Cronquist, A.

1981. *An integrated system of classification of flowering plants*. Columbia University Press, New York, 1262 pp.

Czeczott, H. and Skirgiello, A.

1959. *The fossil flora of Turow near Bogatynia I and II (1), Dicotyledones*. Prace Muzeum Ziemi, vol. 3, pp. 94–112, 121–128.

Daghlian, C. P.

1978. *Coryphoid palms from the lower and middle Eocene of southeastern North America*. Palaeontographica, Abt. B, vol. 166, pp. 44–82, 15 pl.

Daghlian, C. P. and Crepet, W. L.

1983. *Oak catkins, leaves and fruits from the Oligocene Catahoula Formation and their evolutionary significance*. American Journal of Botany, vol. 70, pp. 639–649.

Daly, D. C.

1989. *Studies in neotropical Burseraceae. II. Generic limits in New World Protieae and Canarieae*. Brittonia, vol. 4, pp. 17–27.

Diels, L.

1910. *Menispermaceae*. Das Pflanzenreich, vol. 46 (IV-94), 345 pp.

Dilcher, D. L.

1971. *A revision of the Eocene flora of southeastern North America*. The Paleobotanist, vol. 20, pp. 7–18.

Dilcher, D. L., and McQuade, J. F.

1967. *A morphological study of* Nyssa *endocarps from Eocene deposits in western Tennessee*. Bulletin of the Torrey Botanical Club, vol. 94, pp. 35–40.

Dorofeev, P. I.

1963. *The Tertiary floras of western Siberia*. Akademia Nauk S.S.S.R., Moscow, 345 pp., 50 pl. (in Russian with English Summary).

1982. *Species determined from fruits. Celtis and Aphananthe*, in Takhtajan, A. and Zhilin, S. [eds.], *Fossil flowering plants of the USSR, vol. 2, Ulmaceae—Betulaceae*. pp. 22–24, Nauka, Leningrad. (in Russian).

Doyle, J. A., Schorn, H. E., Tiffney, B. H., and Upchurch, G. R., Jr.

1988. *The LaPorte flora-earliest Oligocene of north-central California*. Field Guide Book for the 1988 meeting of the Paleobotanical Section of the Botanical Society of America, Davis, California, August 14, 1988.

Drinnan, A. N., Crane, P. R., Friis, E. M., and Pedersen, K. R.

1990. *Lauraceous flowers from the Potomac Group (mid-Cretaceous) of eastern North America*. Botanical Gazette, vol. 151, pp. 370–384.

Dupler, A. W.

1920. *Ovuliferous structures of* Taxus canadensis. Botanical Gazette, vol. 69, pp. 492–519.

Endress, P. K.

1989a. *A suprageneric taxonomic classification of the Hamamelidaceae*. Taxon, vol. 38, pp. 371–376.

1989b. *Aspects of evolutionary differentiation of the Hamamelidaceae and the Lower Hamamelididae*. Plant Systematics and Evolution, vol. 162, pp. 193–211.

1989c. *Phylogenetic relationships in the Hamamelidoideae*, in Crane, P. R. and Blackmore, S. [eds.]. *Evolution, Systematics, and fossil history of the Hamamelidae*, Volume 1: 'Lower' Hamamelidae. Systematics Association Special Volume no. 40B, pp. 227–248, Clarendon Press, Oxford, England.

Endress, P. K. and Friis, E. M.

1990. Archamamelis, *hamamelidalean flowers from the Upper Cretaceous of Sweden*. Plant Systematics and Evolution, vol. 175, pp. 101–114.

Engler, A.

1897. *Icacinaceae*. III, Abt. 5. Die natürlichen Pflanzenfamilien, 1 aufl. Leipzig.

1964. *Syllabus der pflanzenfamilien*. 12 ed., Vol. 2. *Angiospermen übersicht über die Florengebiete der Erde*. Gebrüder Borntraeger, Berlin.

Erwin, D. M.

1987. *Silicified palm remains from the Middle Eocene (Allenby Formation) of British Columbia* [abs.]. American Journal of Botany, vol. 74, p. 681.

Evernden, J. F., Savage, D. E., Curtis, G. H., and James, G. T.

1964. *Potassium-argon dates and the Cenozoic mammalian chronology of North America*. American Journal of Science, vol. 262, pp. 145–198.

Eyde, R. H.

1963. *Morphological and paleobotanical studies of the Nyssaceae, I. a survey of the modern species and their fruits*. Journal of the Arnold Arboretum, vol. 44, pp. 1–54, 5 pl.

1968. *Flowers, fruits, and phylogeny of the Alangiaceae*. Journal of the Arnold Arboretum, vol. 49, pp. 167–192.

1988. *Comprehending Cornus: Puzzels, and progress in the systematics of the dogwoods*. Botanical Review, vol. 54, pp. 233–351.

Eyde, R. H., and Barghoorn, E. S.

1963. *Morphological and paleobotanical studies of the Nyssaceae, II: the fossil record*. Journal of the Arnold Arboretum, vol. 44, pp. 328–370.

Eyde, R. H., Bartlett, A., and Barghoorn, E. S.
1969. *Fossil record of* Alangium. Bulletin of the Torrey Botanical Club, vol. 96, pp. 288–314.

Eyde, R. H. and Q., Xiang.
1990. *Fossil mastixioid (Cornaceae) alive in eastern Asia.* American Journal of Botany, vol. 77, pp. 689–692.

Fiebelkorn, R. B., Walker, G. W., MacLeod, N. S., McKee, E. H., and Smith, J. G.
1983. *Index to K-Ar age determinations for the State of Oregon.* Isocron/West, vol. 37, pp. 1–60.

Forman, L. L.
1966. *Generic delimitation in the Castaneoideae.* Kew Bulletin, vol. 18, pp. 421–426.
1974. *The endocarps of* Cocculus *(Menispermaceae).* Kew Bulletin, vol. 29, pp. 477–481.
1985. *A revision of the tribe Fibraureae (Menispermaceae) in Asia. The Menispermaceae of Malesia and adjacent areas XIII.* Kew Bulletin, vol. 40, pp. 539–551.
1986. *Menispermaceae.* Flora Malesiana, ser. I, vol. 102, pp. 157–253.

Foster, S. A.
1986. *On the adaptive value of large seeds for tropical moist forest trees: a review and synthesis.* Botanical Review, vol. 52, pp. 260–299.

Foster, S. A. and Janson, C. H.
1985. *The relationship between seed size and establishment conditions in tropical woody plants.* Ecology, vol. 66, pp. 773–780.

Friis, E. M.
1979. *The Damgaard flora: a new Middle Miocene flora from Denmark.* Bulletin of the Geological Society of Denmark, vol. 27, pp. 117–142.
1985. *Angiosperm fruits and seeds from the Middle Miocene of Jutland (Denmark).* Biologiske Skrifter Det Kongelige Danske Videnskaberne Selskab, vol. 24, pp. 1–165.

Friis, E. M., Crane, P. R., and Pedersen, K. R.
1988. *Reproductive structures of Cretaceous Platanaceae.* The Royal Danish Academy of Sciences and Letters Biologiske Skrifter, vol. 31, pp. 1–55.

Geissert, F. and Gregor, H.-J.
1981. *Einige interessante und neue sommergrüne Pflanzenelemente (Fruktifikationen) aus dem Elsässer Pliozän (*Sabia *Colebr.,* Wikstroemia *Endl.,* Alangium *Lam.,* Nyssa *L.,* Halesia *Ellis,* Rehderodendron *Hu).* Mitteilungen des badischen Landesvereins Naturkunde und Naturschutz, vol. 12, pp. 233–239.

Gentry, A. H.
1983. *Dispersal ecology and diversity in Neotropical forest communities.* Sonderband Naturwissenshaftlichen Vereins in Hamburg, vol. 7, pp. 303–314.
1992. *The distribution and evolution of climbing plants,* in F. E. Putz, and Mooney, H. A. [eds.], *The biology of vines,* pp. 3–43, Cambridge University Press, New York.

Gregor, H.-J.
1978. *Die miozänen Frucht-und Samen-Floren der Oberpfälzer Braunkohle. I. Funde aus den sandigen Zwischenmitteln.* Palaeontographica, Abt. B, vol. 167, pp. 1–103.
1978. Schizandra geissertii *nova spec.—ein exotisches Element im Elsässer Pliozän (Sessenheim, Brunssumien).* Mitteilungen des badischen Landesvereins Naturkunde und Naturschutz, vol. 12, pp. 241–247.

Gregory, I.
1969. *Fossilized palm wood in Oregon.* Ore Bin, vol. 31, pp. 93–110.

Greuter, W., editorial chairman.
1988. *International Code of Botanical Nomenclature.* Adopted by the 14th International Botanical Congress, Berlin, Koeltz Scientific Books, Konigstein, 328 pp.

Grote, P. J.
1989. *Selected fruits and seeds from the Middle Eocene Claiborne Formation of southeastern North America.* PhD dissertation, Indiana University, Bloomington, Indiana 233 pp.

Grote, P. J. and Dilcher, D. L.
1989. *Investigations of angiosperms from the Eocene of North America: a new genus of Theaceae based on fruit and seed remains.* Botanical Gazette, vol. 150, pp. 190–206.

Grudzinskaya, I. A.
1967. *Ulmaceae and reasons for distinguishing Celtidaceae as a separate family Celtidaceae Link.* Botanicheskii Zhurnal, vol. 52, pp. 1723–1748.

Gunn, C. R.
1984. *Fruits and seeds of genera in the subfamily Mimosoideae (Fabaceae).* U.S. Department of Agriculture, Agricultural Research Service, Technical Bulletin 1861, 194 pp.
1991. *Fruits and seeds of genera in the subfamily Caesalpinioideae (Fabaceae).* U.S. Department of Agriculture, Agricultural Research Service, Technical Bulletin 1755, 408 pp.

Hammel, B. E., and Zamora, N. A.
1990. Nyssa talamancana *(Cornaceae) an addition to the remnant Laurasian Tertiary flora of southern Central America.* Brittonia, vol. 43, pp. 165–170.

Hanson, C. B.
1973. *Geology and vertebrate faunas in the type area of the Clarno Formation, Oregon. Geological Society of America, Cordilleran Section Abstracts with Programs,* vol. 5, pp. 50.
1991. Telataceras radinskyi, *a new primitive rhinocerotid from the late Eocene Clarno Formation, Oregon,* in Prothero, D. R. and Schoch, R. M. [eds.], *The Evolution of Perissodactyls,* pp. 379–398, Oxford Monographs on Geology and Geophysics. Oxford University Press, New York.

Herendeen, P. S.
1991. *Lauraceous wood from the mid-Cretaceous Potomac Group of eastern North America:* Paraphyllanthoxylon marylandense *sp. nov.* Review of Palaeobotany and Palynology, vol. 69, pp. 277–290.

Herendeen, P. S. and Dilcher, D. L.
1990. *Fossil mimosoid legumes from the Eocene and Oligocene of southeastern North America.* Review of Palaeobotany and Palynology, vol. 62, pp. 339–361.

Hergert, H. L.
1961. *Plant fossils in the Clarno Formation, Oregon.* Ore Bin, vol. 23, pp. 55–62.

Hill, A. W.
1933. *The method of germination of seeds enclosed in a stony endocarp.* Annals of Botany, vol. 47, pp. 873–887.
1937. *The method of germination of seeds enclosed in a stony endocarp. II.* Annals of Botany (New Series), vol. 1, pp. 239–256.

Hollick, A.
1936. *The Tertiary floras of Alaska.* U.S. Geological Survey Professional Paper 182, pp. 1–185.

Holý, F.
1975. *Representatives of the family Mastixiaceae Calestani 1905 in the Bohemian Tertiary.* Sborník Národního Musea v Praze; Acta Musei Nationalis Pragae, vol. 31B, pp. 123–147, pl. 1–4.

Howard, R. A.

1942. *Studies of the Icacinaceae IV: Consideration of the New World genera.* Contributions of the Gray Herbarium, vol. 142, pp. 1–60.

Huzioka, K. and Takahasi, E.

1970. *The Eocene flora of the Ube Coal-field, southwest Honshu, Japan.* Journal of the Mining College of Akita University, Ser. A, vol. 4, no. 5, pp. 1–88.

Jähnichen, H.

1976. *Schisandraceae und Illiciaceae als holarktische und subtropische Florenelemente im mitteleuropäischen Alttertiär.* Abhandlungen des Zentralen Geologischen Instituts Paläontologische Abhandlungen, vol. 26, pp. 151–197, pl. 8–18.

Jain, R. K.

1963. *Studies in Musaceae—I.* Musa cardiosperma *sp. nov., a fossil banana fruit from the Deccan Intertrappean Series, India.* The Palaeobotanist, vol. 12, pp. 45–58, pl. 1–4.

1965. *Studies in Musaceae III. Fossil records of Musaceae and the Origin of Bananas.* Proceedings of the Indian Academy of Science, vol. 61, pp. 170–179.

Jones, J. H. and Dilcher, D. L.

1980. *Investigations of angiosperms from the Eocene of North America:* Rhamnus marginatus *(Rhamnaceae) reexamined.* American Journal of Botany, vol. 67, pp. 959–967.

Kapil, R. N. and Jalan, S.

1964. Schisandra *Michaux—it embryology and systematic position.* Botaniska Notiser, vol. 117, pp. 285–306.

Kaul, R. B.

1988. *Cupular structure in paleotropical* Castanopsis *(Fagaceae).* Annals of the Missouri Botanical Garden, vol. 75, pp. 1480–1498.

1989. *Fruit structure and ecology in paleotropical Lithocarpus (Fagaceae),* in Crane, P. R. and Blackmore, S. [eds.]. *Evolution, Systematics, and fossil history of the Hamamelidae,* Volume 2: 'Higher' Hamamelidae. Systematics Association Special Volume no. 40B, pp. 67–86, Clarendon Press, Oxford, England.

Kirchheimer, F.

1936. *Zur Kentniss der Früchte rezenter und fossiler Mastixioideen.* Beihefte zum Botanischen Centralblatt, vol. 55, pp. 275–300, pl. 5–8.

1938. *Beiträge zur näheren Kenntnis von Vitaceen-Samenformen tertiären Alters.* Planta, vol. 28, pp. 582–598, pl. 5–8.

1940. *Die Mastixioideenflora der altertiären Braunkohlenschichten von Wiesa bei Kamenz (Sachsen).* 10 Jahresheft (1940) der Naturwissenschaftlichen Gesellshaft Isis in Kamenz, C.S. Krausche, Kamenz (Sachsen), 32 pp.

1949. *Die Symplocaceae der erdgeschichtlichen Vergangenheit.* Palaeontographica, Abt. B, vol. 90, pp. 1–52, pl. 1–2.

1957. Die Laubgewächse der Braunkohlenzeit. Veb Wilhelm Knapp Verlag, Halle (Salle), 783 pp.

Knobloch, E. and Mai, D. H.

1986. *Monographie der Früchte und Samen in der Kreide von Mitteleuropa.* Vydal Ustřední ústav geologický, vol. 47, pp. 219, 56 pl.

Kovacs, E.

1957. Dracontomelon minimum *Reid-Chandler aus den Eozän-Kohlenschichten von Tatabanya.* Földtany Közlöny; Bulletin of the Hungarian Geological Society, vol. 87, pp. 215–217.

Krause, J.

1942. *Staphyleaceae.* Die Natürlichen Pflanzenfamilien, 2, vol. 206, pp. 255–321.

Krützsch, W.

1976. *Die Mikroflora der Braunkohle des Geiseltales, Teil IV: Die stratigraphische Stellung des Geiseltalprofils im Eozän und die sporenstratigraphische Untergliederung des mittleren Eozäns.* Abhandlungen des Zentralen Geologischen Instituts Berlin vol. 26, pp. 47–92.

1989. *Paleogeography and historical phytogeography (paleochorology) in the Neophyticum.* Plant Systematics and Evolution, vol. 162, pp. 5–61.

Kvaček, Z.

1982. *Tertiary taxads of NW Bohemia.* Acta Universitatis Carolinae—Geologica, Pokornyaa, vol. 4, pp. 471–491.

Kvaček, Z., Bůžek, Č., and S. R. Manchester.

1991. *Fossil fruits of* Pteleaecarpum *Weyland—Tiliaceous not sapindaceous.* Botanical Gazette, vol. 152, pp. 522–523.

Kvaček, Z. and Walther, H.

1989. *Paleobotanical studies in Fagaceae of the European Tertiary.* Plant Systematics and Evolution, vol. 162, pp. 213–229.

Lam, H. J.

1931. *Beiträge zur Morphologie der dreizähligen Burseraceae-Canarieae.* Annales du jardin botanique de Buitenzorg, vol. 42, pp. 23–56, 3 pl.

1932. *Beiträge zur Morphologie der Burseraceae. Inbesondere der Canarieae.* Annales du jardin botanique de Buitenzorg, vol. 42, pp. 97–226, 6 pl.

Laurent, L.

1912. *Flore fossile des schistes de Menat (Puy-de-Dôme).* Annales du Musée d'Histoire Naturelle de Marseille, vol. 14, pp. 1–246.

Lesquereux, L.

1878. *Contributions to the flora of the Western Territories II. The Tertiary flora.* Report of the U.S. Geological Survey of the Territories, vol. 7, pp. 1–366.

Lockwood, E. H. and MacMillan, R. H.

1978. *Geometric symmetry.* Cambridge University Press, Cambridge, England, 228 pp.

Mabberley, D. J.

1989. *The plant-book.* Cambridge University Press, Cambridge, England, 706 pp.

MacGinitie, H. D.

1969. *The Eocene Green River flora of northwestern Colorado and northeastern Utah.* University of California Publications in Geological Sciences, vol. 83, 203 pp., 31 pl.

1974. *An early Middle Eocene flora from the Yellowstone-Absaroka Volcanic Province, northwestern Wind River Basin, Wyoming.* University of California Publications in Geological Sciences, vol. 108, 103 pp., 45 pl.

Magallón-Puebla, S. and Cevallos-Ferriz, S. R. S.

1992. Cedrelospermum *(Ulmaceae) fruits from Upper Cenozoic Strata of Puebla, Mexico.* American Journal of Botany, vol. 79(6), p. 103. Abstract.

Mai, D. H.

1970. *Subtropische Elemente im europäischen Tertiär I. Die Gattungen* Gironniera, Sarcococca, Illicium, Evodia, Ilex, Mastixia, Alangium, Symplocos *und* Rehderodendron. Paläontologische Abhandlungen Abt. B, vol. 3, pp. 441–503, pl. 58–69.

1971. *Über fossile Lauraceae und Theaceae in Mitteleuropa.* Feddes Repertorium, vol. 82, pp. 313–341.

1975. *Beiträge zur Bestimmung und Nomenklatur fossiler Magnolien.* Feddes Repertorium, vol. 86, pp. 559–578.

1976. *Fossile Früchte und Samen aus dem Mitteleozän des Gei-*

seltales. Abhandlungen des Zentralen Geologischen Instituts Berlin, vol. 26, pp. 93–149, pl. 1–7.

1980. *Zur Bedeutung von Relikten in der Florengeschichte*. 100 Jahre Arboretum (1879–1979), pp. 281–307.

1984. *Karpologische Untersuchungen der Steinkerne fossiler und rezenter Amygdalaceae (Rosales)*. Feddes Repertorium, vol. 95, pp. 299–329, pl. 29–50.

1985. *Beiträge zur Geschichte einiger holziger Saxifragales-Gattungen*. Gleditschia, vol. 13, pp. 75–88.

1986. *Über antillanische Symplocaceae*. Feddes Repertorium, vol. 97, pp. 1–28.

1987. *Neue Früchte und Samen aus paläozänen Ablagerungen Mitteleuropas*. Feddes Repertorium, vol. 98, pp. 197–229, pl. 12–21.

1989. *Development and regional differentiation of the European vegetation during the Tertiary*. Plant Systematics and Evolution, vol. 162, pp. 79–91.

Mai, D. H. and Walther, H.

1978. *Die Floren der Haselbacher Serie im Weisselster-Becken (Bezirk Leipzig, DDR)*. Abhandlungen der Staatliches Museums für Mineralogie und Geologie, vol. 28, 200 pp., 50 pl.

1988. *Die pliozänen Floren von Thüringen, Deutsche Demokratische Republik*. Quartärpaläontologie, vol. 7, pp. 55–297, 41 pl.

Manchester, S. R.

1976. *Description and interpretation of fossil woods, leaves and fruits from the Clarno Nut Beds, Wheeler County, Oregon*. Oregon Museum of Science and Industry Technical Reports, vol. 4, pp. 65–102.

1977. *Wood of* Tapirira *(Anacardiaceae) from the Paleogene Clarno Formation of Oregon*. Review of Palaeobotany and Palynology, vol. 23, pp. 119–127.

1979. Triplochitioxylon *(Sterculiaceae): A new genus of wood from the Eocene of Oregon and its bearing on xylem evolution in the extant genus Triplochiton*. American Journal of Botany, vol. 66, pp. 699–708.

1980. Chattawaya *(Sterculiaceae): A new genus of wood from the Eocene of Oregon and its implications for xylem evolution of the extant genus* Pterospermum. American Journal of Botany, vol. 67, pp. 59–67.

1981. *Fossil plants of the Eocene Clarno Nut Beds*. Oregon Geology, vol. 43, pp. 75–81.

1983. *Fossil wood of the Engelhardieae (Juglandaceae) from the Eocene*: Engelhardioxylon *gen. nov*. Botanical Gazette, vol. 144, pp. 157–163.

1986. *Vegetative and reproductive morphology of an extinct plane tree (Platanaceae) from the Eocene of western North America*. Botanical Gazette, vol. 147, pp. 200–226.

1987a. *The fossil history of the Juglandaceae*. Monographs in systematic botany from the Missouri Botanical Garden, vol. 21, pp. 1–137.

1987b. *Extinct ulmaceous fruits from the Tertiary of Europe and western North America*. Review of Palaeobotany and Palynology, vol. 52, pp. 119–129.

1988. *Fruits and seeds of* Tapiscia *(Staphyleaceae) from the middle Eocene of Oregon, USA*. Tertiary Research, vol. 9, pp. 59–66.

1989a. *Attached reproductive and vegetative remains of the extinct American-European genus* Cedrelospermum *(Ulmaceae) from the Early Tertiary of Utah and Colorado*. American Journal of Botany, vol. 76, pp. 256–276.

1989b. *Early history of the Juglandaceae*. Plant Systematics and Evolution, vol. 162, pp. 231–350.

1989c. *Systematics and fossil history of the Ulmaceae*, in Crane, P. R. and Blackmore, S. [eds.]. *Evolution, Systematics, and fossil history of the Hamamelidae*, Volume 2: 'Higher' Hamamelidae. Systematics Association Special Volume no. 40B, pp. 221–252, Clarendon Press, Oxford, England.

1990. *Eocene to Oligocene floristic changes recorded in the Clarno and John Day Formations, Oregon, USA*, in E. Knobloch, and Kvaček, Z., [eds.], *Symposium Proceedings, paleofloristic and paleoclimatic changes in the Cretaceous and Tertiary*, pp. 183–187, Geological Survey Press, Prague, Czechoslovakia.

1991. Cruciptera, *a new juglandaceous winged fruit from the Eocene and Oligocene of western North America*. Systematic Botany, vol. 16, pp. 715–725.

Manchester, S. R. and Crane, P. R.

1983. *Attached leaves, inflorescences, and fruits of* Fagopsis *an extinct genus of fagaceous affinity from the Oligocene Florissant flora of Colorado, U.S.A*. American Journal of Botany, vol. 70, pp. 1147–1164.

Manchester, S. R. and Meyer, H. W.

1987. *Oligocene fossil plants from the John Day Formation, Fossil, Oregon*. Oregon Geology, vol. 49, pp. 115–127.

Manchester, S. R. and Miller, R. B.

1978. *Tile cells and their occurrence in malvalean fossil woods*. IAWA Bulletin, vol. of 1978, pp. 23–28.

Manchester, S. R. and Wheeler, E. A.

1993. *Extinct juglandaceous wood from the Eocene of Oregon and its implications for xylem evolution in the Juglandaceae*. IAWA Journal, vol. 14, pp. 103–111.

Manchester, S. R. and Zavada, M. S.

1987. Lygodium *foliage with intact sorophores from the Eocene of Wyoming*. Botanical Gazette, vol. 148, pp. 392–399.

Manchester, S. R. and Kress, W. J.

1993. *Fossil bananas (Musaceae)*: Ensete oregonense *sp. nov. from the Eocene of western North America and its phytogeographic significance*. American Journal of Botany, vol. 80, pp. 1264–1272.

Mathewes, R. and Brooke, R. C.

1971. *Fossil Taxodiaceae and new angiosperm macrofossils from Quilchena, British Columbia*. Syesis, vol. 4, pp. 209–216.

Matthew, K. M.

1976. *A revision of the genus* Mastixia *(Cornaceae)*. Blumea, vol. 23, pp. 51–93.

Mazer, S. J. and Tiffney, B. H.

1982. *Fruits of* Wetherellia *and* Palaeowetherellia *(? Euphorbiaceae) from Eocene sediments in Virginia and Maryland*. Brittonia, vol. 34, pp. 300–333.

McClintock, E.

1957. *A monograph of the genus* Hydrangea. Proceedings of the California Academy of Sciences, fourth series, vol. 29, pp. 147–256.

McGahan, M. W.

1961. *Studies on the seed of banana. I. Anatomy of the seed and embryo of* Musa balbisiana. American Journal of Botany, vol. 48, pp. 230–238.

McKee, T. M.

1970. *Preliminary report on fossil fruits and seeds from the Mammal Quarry of the Clarno Formation, Oregon*. Ore Bin, vol. 32, pp. 117–132.

McKenna, M. C.

1975. *Fossil mammals and early Eocene North Atlantic land continuity*. Annals of the Missouri Botanical Garden, vol. 62, pp. 335–353.

Mellet, J. S.

1969. *A skull of* Hemipsalidon *(Mammalia Deltatheridia) from the Clarno Formation of Oregon.* Novitates, American Museum of Natural History, no. 2387, pp. 1–19.

Metcalfe, D. R. and Chalk, L.

1950. *Anatomy of the Dicotyledons.* Clarendon Press, Oxford, 2 vol., 1500 pp.

Meyer, H. W.

1992. *Lapse rates and other variables applied to estimating paleoaltitudes from fossil floras.* Palaeogeography, Palaeoclimatology, Palaeoecology, vol. 99, pp. 71–99.

Mohana Rao, P. R.

1974. *Seed anatomy in some Hamamelidaceae and phylogeny.* Phytomorphology, vol. 24, pp. 113–139.

Morgan, D. R. and Soltis, D. E.

1993. *Phylogenetic relationships among members of Saxifragaceae sensu lato based on rbcL sequence data.* Annals of the Missouri Botanical Garden, vol. 80, pp. 631–660.

Muller, J. and Leenhouts, P. W.

1976. *A general survey of pollen types in Sapindaceae in relation to taxonomy,* in Ferguson, I. K. and Muller, J. [eds.], *The evolutionary significance of the exine,* pp. 407–445. Academic Press, London.

Nilsen, T. H. and McKee, E. H.

1979. *Paleogene paleogeography of the western United States,* in J. M. Armentrout, Cole, M. R., and TerBest, H., Jr. [eds.], *Cenozoic paleogeography of the western United States.* pp. 257–276, Pacific Coast Paleogeography Symposium 3. Pacific Section, SEPM.

Nixon, K. C.

1989. *Origins of Fagaceae,* in Crane, P. R. and Blackmore, S. [eds.]. *Evolution, Systematics, and fossil history of the Hamamelidae,* Volume 2: 'Higher' Hamamelidae. Systematics Association Special Volume no. 40B, pp. 23–44, Clarendon Press, Oxford, England.

Noblett, J. B.

1981. *Subduction-related origin of the volcanic rocks of the Eocene Clarno Formation near Cherry Creek, Oregon.* Oregon Geology, vol. 43, pp. 91–99.

Nooteboom, H. P.

1975. *Revision of the Symplocaceae of the Old World New Caledonia excepted.* Universitair Pers Leiden, The Netherlands, 335 pp.

1985. *Notes on Magnoliaceae with a revision of* Pachylarnax *and* Elmerrillia *and the Malesian species of* Manglietia *and* Michelia. Blumea, vol. 31, pp. 65–121.

Parrish, J. T.

1987. *Global palaeogeography and palaeoclimate of the Late Cretaceous and Early Tertiary,* in E. M. Friis, Chaloner, W. G., and Crane, P. R. [eds.], *The origins of angiosperms and their biological consequences,* pp. 51–73. Cambridge University Press, Cambridge, England.

Pigg, K. A. and Stockey, R. A.

1991. *Platanaceous plants from the Paleocene of Alberta, Canada.* Review of Palaeobotany and Palynology, vol. 70, pp. 125–146.

Potbury, S. S.

1935. *The La Porte flora of Plumas County, California.* Carnegie Institute of Washington Publication 465, pp. 29–82, pl. 1019.

Radlkofer, L.

1890. *Ueber die Gliederung der Familie der Sapindaceae.* Sitzungsberichte der mathemathematisch-physikalischen Classe de Bayerische Akademie Wissenschaften München, vol. 20, pp. 105–379.

Reid, E. M. and Chandler, M. E. J.

1933. *The London Clay Flora.* British Museum (Natural History), London, England, vii + 561 pp., 33 pl.

Retallack, G.

1981. *Preliminary observations on fossil soils in the Clarno Formation (Eocene to early Oligocene) near Clarno, Oregon.* Oregon Geology, vol. 43, pp. 147–150.

1991. *A field guide to mid-Tertiary paleosols and paleoclimatic changes in the high desert of central Oregon—Part 1.* Oregon Geology, vol. 55, pp. 51–59.

Rogers, J. J. W. and Novitsky-Evans, J. M.

1977. *The Clarno Formation of central Oregon, U.S.A.—volcanism on a thin continental margin.* Earth and Planetary Science Letters, vol. 34, pp. 56–66.

Rohrer, J. R., Robertson, K. R., and Phipps, J. B.

1991. *Variation in structure among fruits of Maloideae (Rosaceae).* American Journal of Botany, vol. 78, pp. 1617–1635.

Roth, J. L., Jr. and Dilcher, D. L.

1979. *Investigations of angiosperms from the Eocene of North America: Stipulate leaves of the Rubiaceae including a probable polyploid population.* American Journal of Botany, vol. 66, pp. 1194–1207.

Rüffle, L.

1976. *Myricaceae, Leguminosae, Icacinaceae, Sterculiaceae, Nymphaeaceae, Monocotyledones, Coniferae. Eozäne Floren des Geiseltals.* Abhandlungen des Zentralen Geologischen Instituts Berlin, vol. 26, pp. 337–438.

Saleeby, J. B.

1983. *Accretionary tectonics of the North American Cordillera.* Annual Review of Earth and Planetary Science, vol. 15, pp. 45–73.

Salisbury, E. J.

1942. *The reproductive capacity of plants. Studies in quantitative biology.* G. Bell and Sons, London, England, 244 pp.

Schaarschmidt, F.

1988. *Der Wald, fossile Pflanzen als Zeugen eines warmen Klima,* in S. Schaal, and Ziegler, W. [eds.] *Messel—Ein Schaufenster in die Geschichte der Erde und des Lebens,* pp. 29–52, W. Kramer, Frankfurt am Main, Germany.

Schenk, E. T. and McMasters, J. H.

1956. *Procedure in Taxonomy.* Stanford University Press, Stanford, California. 3rd ed., 119 pp.

Schmid, R.

1986. *On cornerian and other terminology of angiospermous and gymnospermous seed coats: Historical perspective and terminological recommendations.* Taxon, vol. 35, pp. 476–491.

Schumann, K.

1897. *Rubiaceae.* in Engler and Prantl, Die natürlichen Pflanzenfamilien. Teil 4, Abteilung 4, pp. 1–194, W. Engelmann, Leipzig.

Scott, A. and Collinson, M. E.

1983. *Investigating fossil plant beds, part 1: the origin of fossil plants and their sediments.* Geology Teaching, vol. 7, pp. 114–122.

Scott, R. A.

1954. *Fossil fruits and seeds from the Eocene Clarno Formation of Oregon.* Palaeontographica, Abt. B, vol. 96, pp. 66–97, pl. 15–16.

1956. *Evolution of some endocarpal features in the tribe Tinosporeae (Menispermaceae).* Evolution, vol. 10, pp. 74–81.

Scott, R. A., Barghoorn, E. S., and Prakash, U.

1962. *Wood of* Ginkgo *in the Tertiary of western North America.* American Journal of Botany, vol. 49, pp. 1095–1101.

Scott, R. A. and Wheeler, E. A.

1982. *Fossil woods from the Eocene Clarno formation of Oregon.* IAWA Bulletin, n.s., vol. 3, pp. 135–154.

Sela, J. and Boyde, A.

1977. *Cyanide removal of gold from SEM specimens.* Journal of Microscopy, vol. 3, pp. 229–231.

Sellick, J. T. C.

In Press. *Phasmid eggs from the Eocene of Oregon.* Palaeontology, vol. 36.

Sleumer, H.

1942. *Icacinaceae.* in Engler and Prantl, Die natürlichen Pflanzenfamilien, 20b. Aufl. 2. Leipzig.

1969. *Materials toward the knowledge of the Icacinaceae of Asia, Malesia, Australia and the Pacific.* Blumea, vol. 17, pp. 181–264.

1971. *Icacinaceae.* Flora Malesiana, ser. I, vol. 7, pp. 1–87.

Smith, A. C.

1947. *The families Illiciaceae and Schisandraceae.* Sargentia, vol. 7, pp. 1–224.

Standley, P. C. and Williams, L. O.

1975. *Flora of Guatemala. Rubiaceae.* Fieldiana Botany, vol. 124, pp. 1–274.

Stirton, R. A.

1944. *A rhinoceros tooth from the Clarno Eocene of Oregon.* Journal of Paleontology, vol. 18, pp. 265–267.

Stockey, R. A.

1984. *Middle Eocene* Pinus *remains from British Columbia.* Botanical Gazette, vol. 74, pp. 1878–1887.

Stockey, R. A. and Crane, P. R.

1983. *In Situ* Cercidiphyllum*-like seedlings from the Paleocene of Alberta,* Canada. American Journal of Botany, vol. 70, pp. 1564–1568.

Sun, F. and Stockey, R. A.

1992. *A new betulaceous plant from the Paleocene of Alberta, Canada.* International Journal of Plant Science, vol. 153, pp. 136–146.

Swanson, D. A. and Robinson, P. T.

1968. *Base of the John Day Formation in and near the Horse Heaven mining district, north-central Oregon.* U.S. Geological Survey Professional Paper 600-D, pp. 154–161.

Takaso, T. and Tobe, H.

1990. *Seed coat morphology and evolution in Celtidaceae and Ulmaceae (Urticales).* Botanical Magazine, Tokyo, vol. 103, pp. 25–41.

Takhtajan, A.

1966. *Major phytochoria of the late Cretaceous and the early Tertiary in USSR and adjacent countries.* 13th Sir Charles Seward Memorial lecture Lucknow, India, 12 pp.

1986. *Floristic regions of the world.* University of California Press, Berkeley, 522 pp.

Tanai, T.

1990. *Euphorbiaceae and Icacinaceae from the Paleogene of Hokkaido, Japan.* Bulletin of the National Science Museum, series C (Geology and Paleontology), vol. 16, pp. 91–118.

Tanai, T. and Wolfe, J. A.

1977. *Revisions of* Ulmus *and* Zelkova *in the middle and late Tertiary of western North America.* U.S. Geological Survey Professional Paper 1026, pp. 1–11.

Taylor, D. W.

1990. *Paleobiogeographic relationships of angiosperms from the Cretaceous and early Tertiary of the North American area.* Botanical Review, vol. 56, pp. 279–417.

Teichman, I., van, and Robbertse, P. J.

1986. *Development and structure of the pericarp and seed of* Rhus lancea *L. fil. (Anacardiaceae), with taxonomic notes.* Botanical Journal of the Linnean Society, vol. 93, pp. 291–306.

Thanikaimoni, G.

1984. *Ménispermacées: Palynologie et Systématique.* Institut Francais de Pondichery Travaux de la Section Scientifique et Technique, Pondichery, India, vol. 18, 135 pp.

1986. Evolution of Menispermaceae. Canadian Journal of Botany, vol. 64, pp. 3130–3133.

Tiffney, B. H.

1977. *Fruits and seeds of the Brandon Lignite: Magnoliaceae.* Botanical Journal of the Linnean Society, vol. 75, pp. 299–323.

1979. *Fruits and seeds of the Brandon Lignite. III.* Turpinia *(Staphyleaceae).* Brittonia, vol. 31, pp. 39–51.

1981. *Fruits and seeds of the Brandon Lignite. VI.* Microdiptera *(Lythraceae).* Journal of the Arnold Arboretum, vol. 62, pp. 487–516.

1984. *Seed size, dispersal syndromes, and the rise of the angiosperms: evidence and hypothesis.* Annals of the Missouri Botanical Garden, vol. 71, pp. 551–576.

1985a. *Perspectives on the origin of the floristic similarity between eastern Asia and eastern North America.* Journal of the Arnold Arboretum, vol. 66, pp. 73–94.

1985b. *The Eocene North Atlantic land bridge: its importance in Tertiary and modern phytogeography of the Northern Hemisphere.* Journal of the Arnold Arboretum, vol. 66, pp. 243–273.

1990. *The collection and study of dispersed angiosperm fruits and seeds.* Palaios, vol. 5, pp. 499–519.

Tiffney, B. H. and Barghoorn, E. S.

1976. *Fruits and seeds of the Brandon Lignite: I. Vitaceae.* Review of Palaeobotany and Palynology, vol. 22, pp. 169–191.

Traverse, A.

1955. *Pollen analysis of the Brandon Lignite of Vermont.* U.S. Bureau of Mines Report of Investigations 5151, 107 pp.

Upchurch, G. R., Jr., and Wolfe, J. A.

1987. *Mid-Cretaceous to Early Tertiary vegetation and climate: evidence from fossil leaves and woods*, in E. M. Friis, Chaloner, W. G., and Crane, P. R. [eds.], *The origins of angiosperms and their biological consequences*, pp. 75–106. Cambridge University Press, Cambridge, England.

Vance, J. A.

1988. *New fission track and K-Ar ages from the Clarno Formation, Challis age volcanic rocks in north central Oregon. Geological Society of America, Rocky Mountain Section Abstracts with Programs*, vol. 20, p. 473.

Walker, G. W.

1977. *Geologic map of Oregon east of the 121st meridian.* U.S. Geological Survey Miscellaneous Investigation Series Map I-902, scale 1:500,000.

Walker, G. W. and Robinson, P. I.

1990. *Paleocene (?) Eocene, and Oligocene (?) rocks of the Blue Mountain Region*, in G.W. Walker, [ed.]. *Geology of the Blue Mountains Region of Oregon, Idaho, and Washington: Cenozoic geology of the Blue Mountains Region.* pp. 13–28. U.S. Geological Survey Professional Paper 1437.

Wang, C.-W.

1961. *The forests of China with a survey of grassland and desert* *vegetation.* Maria Moors Cabot Foundation publication no. 5, Cambridge, Massachusetts, 313 pp.

Welzen, P. C., van

1988. *Key to the Malesian genera of Sapindaceae (based on vegetative and fruit characteristics).* Blumea, vol. 33, pp. 215–237.

Werff, H., van der

1991. *A key to the genera of Lauraceae in the New World.* Annals of the Missouri Botanical Garden, vol. 78, pp. 377–387.

Wheeler, E. and Baas, P.

1992. *Fossil wood of the Leguminosae: a case study in xylem evolution and ecological anatomy*, in Herendeen, P. S. and Dilcher, D. L. [eds.], *Advances in Legume systematics part 4 the fossil record*, pp. 281–302, Royal Botanic Gardens, Kew, England.

Wilde, V.

1989. *Untersuchunge zur Systematik der Blattreste aus dem Mitteleozän der Grube Messel bei Darmstadt (Hessen, Bundesrepublik Deutschland).* Courier Forschungsinstitut Senckenberg, vol. 115, pp. 1–213.

Wing, S. L.

1988. *Eocene and Oligocene floras and vegetation of the Rocky Mountains.* Annals of the Missouri Botanical Garden, vol. 74, pp. 748–784.

Wing, S. L. and Hickey, L. H.

1984. *The* Platycarya *perplex and the evolution of the Juglandaceae.* American Journal of Botany, vol. 71, pp. 388–411.

Wolfe, J. A.

1968. *Paleogene biostratigraphy of nonmarine rocks in King County, Washington.* U.S. Geological Survey Professional Paper 571, pp. 1–33.

1971. *Tertiary climatic fluctuations and methods of analysis of Tertiary floras.* Palaeogeography, Palaeoclimatology, Palaeoecology, vol. 9, pp. 27–57.

1972. *An interpretation of Alaskan Tertiary floras* in *Floristics and Paleofloristics of Asia and eastern North America*, in Graham, A. [ed.], *Floristics and Paleofloristics of Asia and eastern North America*, pp. 201–233, Elsevier, Amsterdam.

1975. *Some aspects of plant geography of the Northern Hemisphere during the Late Cretaceous and Tertiary.* Annals of the Missouri Botanical Garden, vol. 62, pp. 264–279.

1977. *Paleogene floras from the Gulf of Alaska Region.* U.S. Geological Survey Professional Paper 997, pp. 1–107.

1979. *Temperature parameters of humid to mesic forests of eastern Asia and relation to forests of other regions in the Northern Hemisphere.* U.S. Geological Survey Professional Paper 1106, pp. 1–37.

1981. *A chronological framework for Cenozoic megafossil floras of northwestern North America and its relation to marine geochronology.* Geological Society of America Special Paper, vol. 184, pp. 39–47.

1985. *Distribution of major vegetational types during the Tertiary*, in *The carbon cycle and atmospheric CO_2: Natural variation, Archaean to Present*, Geophysical Monograph 32, pp. 357–375.

Wolfe, J. A. and Hopkins, D. M.

1967. *Climatic changes recorded by Tertiary land floras in Northwestern North America*, in K. Hatai, [ed.], *Tertiary Correlations and Climatic Changes in the Pacific, 11th Pacific Science Congress of the Pacific Science Association, Tokyo*, vol. 25, pp. 67–76.

Wolfe, J. A. and Poore, R. Z.

1982. *Tertiary marine and nonmarine climatic trends*, in W. Berger, and Crowell, J.C. [eds.]. *Climate in Earth history*, pp. 154–158, National Academy of Science, Studies in Geophysics, Washington, D.C.

Wolfe, J.A. and Tanai, T.

1987. *Systematics, phylogeny, and distribution of* Acer *(maples) in the Cenozoic of western North America.* Journal of the Faculty of Science, Hokkaido University, vol. 22, pp. 1–246.

Wolfe, J. A. and Upchurch, G. A., Jr.

1986. *Vegetation, climatic, and floral changes at the Cretaceous-Tertiary boundary.* Nature, vol. 324, pp. 148–151.

Wolfe, J. A. and Wehr, W.

1987. *Middle Eocene dicotyledonous plants from Republic, Northeastern Washington.* U.S. Geological Survey Bulletin 1597, pp. 1–25.

Wu T.-L.

1981. *Musaceae, Zingiberaceae, Cannaceae, Marantaceae, Burmanniaceae.* Flora Reipublicae Popularis Sinicae, vol. 16 (2) Science Press, Beijing, pp. 1–189.

Xiang, Qiu-Yun, Soltis, D. E., Morgan, D. R., and Soltis, P. S.

1993. *Phylogenetic relationships of* Cornus *L. sensu lato and putative relatives inferred from rbcL sequence data.* Annals of the Missouri Botanical Garden, vol. 80, pp. 723–734.

Zona, S.

1990. *A monograph of* Sabal *(Arecaceae: Coryphoideae).* Aliso, vol. 12, pp. 583–666.

EXPLANATION OF PLATE 1*

Figure	Page
1. *Equistetum clarnoi* Brown strobilus showing hexagonal sporangiophores. OMSI-Pb 582. RL, ×3.	15
2. Eroded pinaceous seed cone. UF 9887. ×1.	30
3. Compressed pollen cone of *Pinus* sp. from West Branch Creek locality 230. Note bulging basal scales for comparison with figs. 6–8. UF 9961. ×1.5.	30
4, 5. Seeds of *Pinus* sp. from Clarno West Branch Creek locality 229c. UF 9959 and 9960. ×1.	30
6–9. *Pinus* sp. Pollen cone. UF 9334.	30
6. Longitudinally fractured specimen, showing basal portion of the cone with bulging scales. RL, ×5.	
7. Same specimen, sectioned longitudinally near the periphery, showing helical arrangement of sporophylls. RL, ×5.	
8. Same, sectioned longitudinally showing thick central axis. RL, ×5.	
9. Longitudinal thin section showing pollen sacs on the abaxial side of the microsporophylls. RL, ×20.	

---

* For explanation of abbreviations used in Plate captions, see p. 30.


1


2


3


4

5

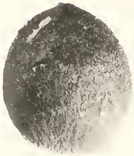

6

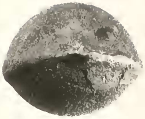

7

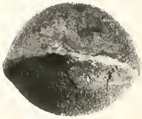

8


9

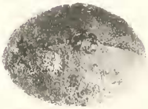

1

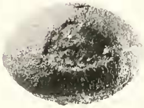

2


3

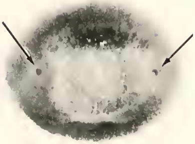

4

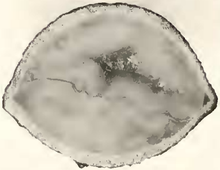

5


6


7


8


9


10

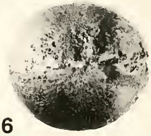

11


12


13


14


15


16

EXPLANATION OF PLATE 2

Figure Page

1–11. *Taxus masonii* sp. nov. 31

1. Seed, lateral view showing pointed apex and truncate base. Holotype, USNM 355474. PC, ×6.
2. Same, face view, showing smooth surface, rounded-obtuse apex, truncate base. PC, ×6.

3, 4. Same, stereo-pair, apical view, showing dorsiventral keel. PC, ×6.4.

5. Seed, lateral view. USNM 355406. PC, ×6.4.
6. Same, apical view, pointed micropylar end. PC, ×6.4.

7, 8. Same, stereo-pair, basal view, showing elliptical truncation with pair of vascular bundle scars. PC, ×6.4.

9. Transverse section near base of the holotype, figs. 1–4, showing the two vascular traces (arrows). USNM 355474. RL, immersed in water, ×20.
10. Same, transverse section midway between base and apex, showing the lensoidal outline and uniform thickness of the seed coat. USNM 355474. RL, ×10.
11. Detail from fig. 10, showing isodiametric cells composing the seed coat. RL, ×50.

12–16. *Torreya clarnensis* sp. nov. PC, ×3. . . 31

12. Seed in face view, showing ovate outline and smooth surface. Holotype, UF 6510.
13. Same, lateral view, showing apical keel and prominent vascular pore (arrow).
14. Another example in face view. Lateral swellings of the margin correspond to the position of the two vascular pores. USNM 422380.
15. Same specimen as in figs. 12, 13, apical view, showing elliptical outline and median keel.
16. Same specimen as in fig. 14, apical view, showing elliptical outline.

EXPLANATION OF PLATE 3

Figure		Page
1–16.	*Diploporus torreyoides* sp. nov.	32

1, 2. Stereo-pair, specimen with aril preserved in the upper half with wrinkled, pitted surface. Seed cast exposed in lower half. USNM 355569. ×5.

3. Same, basal view, showing thickness of the aril, which is partially broken away revealing smooth seed cast within. ×5.

4. Same, apical view, showing micropylar aperture and wrinkly outer surface of the aril. ×5.

5. Internal mold of seed coat, face view, showing wide-elliptical outline and faint longitudinal striations. UF 8541. PC, ×5.

6. Seed in lateral view showing longitudinal striations of the aril, rounded base, dorsiventral keel extending over the apex and vascular pore (arrow). Holotype, UF 8542. PC, ×5.

7. Same, apical view, showing elliptical outline, dorsiventral keel and central micropyle. PC, ×5.

8. Same, basal view, showing smooth surface and pair of pores representing vascular scars (arrows). PC, ×5.

9. Seed in face view. UF 8529. PC, ×4.5.

10. Same, lateral view. PC, ×4.5.

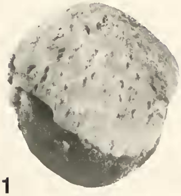
11, 12. Same, stereo-pair, basal view, showing the smooth contours and the pair of lateral pores. PC, ×4.5.

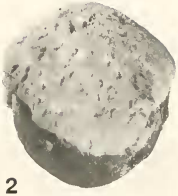
13. Median longitudinal section in the dorsiventral plane showing seed coat and the two lateral pores (arrows). UF 8513. Etched, RL, ×5.

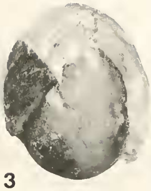
14. Median longitudinal section in the dorsiventral plane of the specimen in fig. 5, showing elongate embryo. Etched, RL, ×4.7.

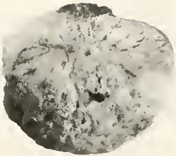
15. Same, enlarged, showing folds of the embryo and speckled appearance of surrounding tissue. Etched, RL, ×10.

16. Transverse section of seed showing circular outline of the embryo in the center and partially intact aril surrounding the seed coat. UF 8514. RL, ×5.

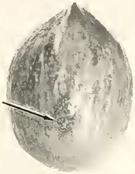

1

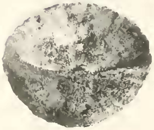

2

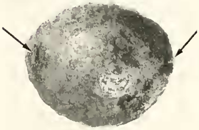

3


4

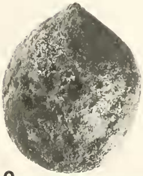

5


6

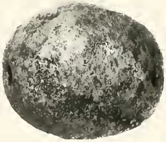

7


8


9


10

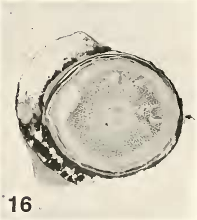

11


12


13

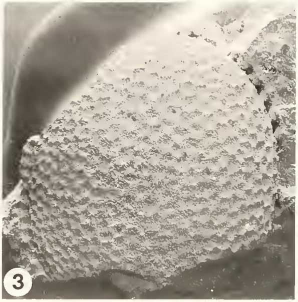

14


15


16

1

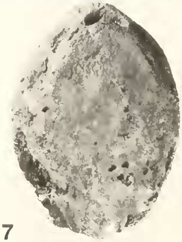

2


3


4


5

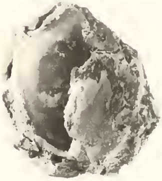

6


7


8


9


10


11


12


13


14


15


16

EXPLANATION OF PLATE 4

Figure Page

1–4. *Actinidia oregonensis* sp. nov. 33

1. Seed cast, lateral view, showing reticulate surface, bluntly pointed micropyle (m) and adjacent hilum (h). Holotype, UF 6292. SEM, ×13.
2. Same, hilar end, showing lensoidal outline of seed. SEM, ×18.
3. Seed cast in matrix. UF 6498. SEM, ×20.
4. Same, enlarged to show space between outer and inner molds of the seed coat. SEM, ×50.

5–14. *Alangium eydei* sp. nov. 34

5. Endocarp cast, face view, showing ovate outline. UF 6508. PC, ×5.
6. Same, lateral view, showing longitudinal septal groove and left carpel slightly larger than right carpel. PC, ×5.
7. Endocarp cast, face view, showing smaller carpel (front) and larger carpel (behind). USNM 422393. PC, ×5.
8. Same, lateral view, showing sculpture of septal wall and one carpel larger than the other. PC, ×5.
9. Locule cast, dorsal view, showing elliptical outline and smooth surface. USNM 424646. PC, ×5.
10. Same, lateral view, showing adjoining locule casts of a fruit with the endocarp wall eroded away, revealing the median septum with arms of the septal canal system emerging as a median row of circular protruberances. PC, ×5.

11, 12. Stereo-pair of a permineralized endocarp, face view, partially broken, revealing one of the locule casts. Holotype, USNM 424646. ×5.

13. Same, transverse section, showing relatively thin wall, median septum perforated by canals, and two locules with remains of the seed coat in each. RL. ×7.
14. Isolated silica cast of the septal canal system. UF 9479. PC, ×5.

15, 16. *Alangium rotundicarpum* sp. nov. Holotype, USNM 435005. 35

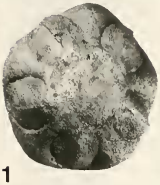
15. Permineralized endocarp, lateral view, showing greater thickness relative to figs. 6, 8. Arms of the septal canal system emerging as a median row of circular protruberances. PC, ×5.
16. Transverse section, showing thick lateral walls and locules virtually equivalent in size. ×7.

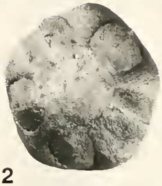
EXPLANATION OF PLATE 5

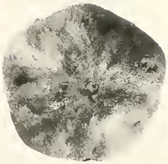
Figure — Page

1–17. *Pentoperculum minimus* (Reid et Chandler) comb. nov. — 36

- 1, 2. Stereo-pair, apical view of fruit, showing rounded pentagonal outline with five elliptical germination valves. USNM 422390. PC, ×5.5.
- 3. Same specimen, basal view, showing small central scar and relatively smooth surface. PC, ×5.5.
- 4. Same, lateral view, showing germination valves in apical half. PC, ×5.5.
- 5. Isolated locule cast, lateral view, showing oblique apical truncation corresponding to the germination valve of the fruit. UF 6664. PC, ×5.
- 6. Same, dorsal view, showing median ridge along the apical truncation. PC, ×5.
- 7–12. Successive transverse sections from apex to base of the specimen in figs. 1–4. RL, ×6.
    - 7. Section near the apex, above the level of locules and central vascular strands.
    - 8. Section showing the central vascular bundles and five locules, each with a pair of shutter-like germination valves (arrows).
    - 9. Nearly equatorial section, showing interlocular lacunae.
    - 10. Equatorial section showing thick outer wall and five locules alternating with five lacunae. Seeds with embryos are preserved in two of the locules.
    - 11. More basal section, below the interlocular lacunae.
    - 12. Basalmost section.
- 13. Transverse section of a fruit in which one of the five germination valves has opened, admitting sediment to the locule. UF 5708. RL, ×6.
- 14. Apical view, specimen from the London Clay flora for comparison with the Clarno fossils. BM v30096. RL, ×5.5.
- 15. Apical view of a rare tetracarpellate specimen. USNM 424851. PC, ×5.5.
- 16. Same, lateral view. PC, ×5.5.
- 17. Same, sectioned longitudinally. RL, ×6.


1


2


3


4


5


6

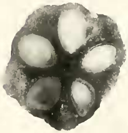

7


8


9

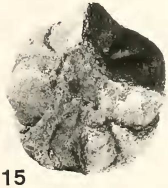

10


11


12


13


14


15

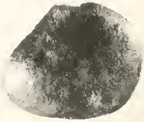

16


17


1


2


3


4


5


6


7


8

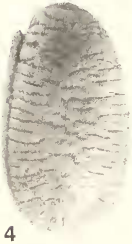

9


10


11


12


13


14


15


16


17


18

Explanation of Plate 6

Figure Page

1–8. *Rhus rooseae* sp. nov. 36

1, 2. Stereo-pair, face view, specimen with longitudinally ribbed meso- and exocarp partially intact. Smooth surface of endocarp exposed at the upper right. Holotype, USNM 355036. RL, ×7.

3. Same, basal view, showing narrow outline and radiating ribs. RL, ×7.

4. Endocarp, face view, showing smooth surface and rounded contours; diagonally broken at upper left. UF 9418. PC, ×7.

5. Same, oblique lateral view, with broken edge showing thick endocarp wall. SEM, ×11.5.

6. Same, enlarged to show circular funicular scar and the layer of anticlinally elongate columnar cells in the endocarp wall. SEM, ×25.

7. Same, more greatly enlarged, showing surface cells of the endocarp arranged in rows radiating from the funicular depression. SEM, ×40.

8. Transverse section showing prominent layer of columnar cells in the endocarp. UF 9420. RL, ×50.

9–15. *Anonaspermum* cf. *pulchrum* Reid et Chandler. PC, ×5. 37

9. Endosperm cast, face view, showing ellipsoidal outline, transverse ruminations and the encircling raphe band. UF 6574.

10. Same, lateral view, showing longitudinal raphe band and transverse ruminations.

11. Same, apical view.

12. Smaller specimen, face view, showing transverse ruminations. UF 5233.

13. Same, lateral view, showing raphe band.

14. Larger specimen, face view, showing raphe band at the margin, transverse ruminations, and radially aligned ruminations near the base. UF 5234.

15. Same, lateral view, showing raphe band partially broken away revealing vascular strand.

16–18. *Anonaspermum bonesii* sp. nov. Holotype, USNM 353975. ×4.5. 38

16, 17. Stereo-pair, endosperm cast, face view, with adhering remains of the seed coat with fibers arranged in a fingerprint pattern.

18. Same, lateral view, showing narrow thickness.

EXPLANATION OF PLATE 7

Figure Page

1, 2. *Anonaspermum rotundum* sp. nov. Holotype, USNM 435099. PC, ×4. 38
1. Face view showing wide elliptical outline and radial arrangement of ruminations.
2. Same, lateral view showing seed thickness and course of the raphe.

3, 4. *Paleopanax oregonensis* gen. et sp. nov. ×5. 38
3. Compressed fruit showing pedicel, D-shaped mericarps, epigynous perianth (arrows) and persistent recurved styles. Holotype, OMSI Pb810.
4. Specimen with larger mericarps and persistent styles. OMSI Pb1779.

5. Extant *Pseudopanax davidii* (Franch.) W.R. Philipson, fruit for comparison with figs. 3 and 4. Western Hupeh, China. E.H. Wilson 1957 (MO). RL, ×5. 38

6–12. *Coryloides hancockii* gen. et sp. nov. 39
6. Chalcedony nut cast, apical view, showing convergence of longitudinal striations toward the stylar projection. UF 8494. PC, ×1.25.
7. Same, basal view, showing outer circular scar of involucre attachment and an inner, more jagged circular scar where vascular strands originating in the involucre passed into the base of the nut. PC, ×1.25.
8. Same, lateral view, showing smooth rounded outline, longitudinal striations, basal involucre scar and apical stylar projection, PC, ×1.25.
9. Nut cast, lateral view, showing longitudinal striations and basal involucre scar. Holotype, UF 8497. PC, ×1.25.
10. Same, basal view, showing jagged-margined circular area where the vascular strands passed into the involucre. PC, ×1.25.
11. Siltstone mold from holotype specimen in figs. 9 and 10, showing prominant longitudinal ribs of vascular strands representing the impression of the outermost fruit layer. RL, ×1.25.
12. Fractured nut with cast of the seed inside, basal view showing shriveled globose seed and circular hilum (arrow) within the fractured nut wall. UF 8498. PC, ×1.25.

13–15. Extant *Corylus* sp. nut with involucre removed for comparison with *Coryloides*. UF mod. ref. coll. 39
13. Lateral view showing globose form, smooth surface with merdional ribs, and prominent basal involucre scar for comparison with figs. 8, 9. RL, ×1.25.
14. Basal view, showing irregular, more or less circular involucre scar with a narrow, zig-zag border for comparison with figs. 7, 10. RL, ×1.25.
15. Transverse section showing wall of nut containing numerous large vascular bundles. RL, ×2.

16–18. *Coryloides hancockii* sp. nov. 39
16. Partially compressed specimen similar to that of fig. 11, showing longitudinal ribs. UF 9898. RL, ×1.25.
17. Same, transversely sectioned, showing prominence of the longitudinal ribs. Contrast with fig. 15. RL, ×2.
18. Same, transverse thin section, showing vascular bundles within the ribs. RL, ×5.

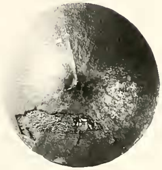

1

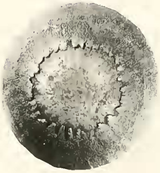

2


3


4

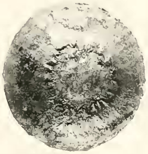

5


6


7

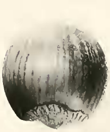

8


9

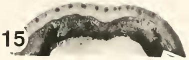

10


11

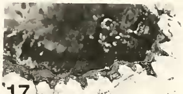

12


13


14


15


16


17


18


1


2


3


4

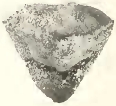

5

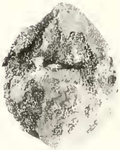

6


7

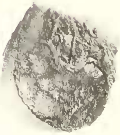

8

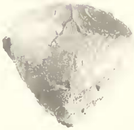

9


10


11


12


13


14


15


16


17


18


19


20

EXPLANATION OF PLATE 8

Figure — Page

1–5. *Kardiasperma parvum* gen. et sp. nov. . . . 40

1. Locule cast, face view, showing median longitudinal groove and pointed apex. Holotype, USNM 435077. SEM, ×23.
2. Another specimen, somewhat wider, face view, showing faintly cordate base. USNM 435076. SEM, ×21.
3. Same as fig. 1, lateral view, showing narrow profile, pointed apex and rounded base. SEM, ×25.
4. Apical view. USNM 424750. SEM, ×21.
5. Basal view. USNM 424076. SEM, ×21.

6–17. *Bursericarpum oregonensis* sp. nov. . . . 40

6. Endocarp, ventral view, showing ovoid outline and transverse placental slit. USNM 424887. PC, ×5.
7. Same, lateral view, showing rounded dorsal margin and ventral notch corresponding to placenta. PC, ×5.

8, 9. Stereo-pair of endocarp, face view, showing transverse placenta and median ventral angle. Holotype, USNM 424885. PC, ×5.

10. Same, apical view, showing triangular outline of the dorsal and ventral faces and the placenta slit seen on the ventral faces. PC, ×5.
11. Endocarp showing ventral placenta and ovoid outline. USNM 434955. PC, ×5.
12. Same, dorsal view, with much of the endocarp wall fractured away, exposing the locule cast. PC, ×5.
13. Chalcedony fruit cast, lateral view, broken apically, with veins of exocarp preserved. USNM 355491. PC, ×5.
14. Same, basal view, showing angle of ventral faces and convex-rounded outline of the dorsal face. PC, ×5.
15. Median longitudinal section showing thickness of endocarp wall. UF 6648. RL, ×7.
16. Locule cast, ventral view showing prominent placental cavity. UF 6663. ×7.
17. Same, apical view. ×7.

18, 19. *Bursericarpum* sp. . . . 41

18. Endocarp, ventral view, showing median ventral angle and transverse placental slit. UF 6655. SEM, ×17.
19. Same, lateral view. SEM, ×17.
20. Betulaceous fruit similar to *Palaeocarpinus* with spiny bract arising from small nutlet similar in size to the locule casts of *Kardiasperma*. West Branch Creek locality 230. UF 9885. ×2.9. . . . 40

EXPLANATION OF PLATE 9

Figure — Page

1–15. *Cornus clarnensis* sp. nov. — 41

1. Endocarp, lateral view showing elliptical outline. Holotype, USNM 422378. PC, ×7.5.

2, 3. Same, stereo-pair, rotated 90°, showing longitudianal vascular grooves. PC, ×7.5.

4. Shorter, wider endocarp, lateral view. USNM 424702. PC, ×7.5.

5. Basal view of holotype as in figs. 1–3, showing circular outline and prominent vascular grooves. PC, ×7.5.

6. Basal view of specimen in fig. 4. PC, ×7.5.

7. Transverse section of specimen in figs. 1–3, and 5, showing two locules. Note absence of a median vascular bundle in the septum. RL, ×10.

8. Transverse section of specimen in figs. 4, 6. RL, ×10.

9–12. Trilocular specimen. USNM 355397.

9. Lateral view, with pericarp partially broken away revealing shiny chalcedony locule cast. PC, ×7.5.

10, 11. Stereo-pair, showing subglobose shape, locule cast seen in dorsal view. PC, ×7.5.

12. Transverse section showing the septum and three locules. RL, ×8.

13. Transverse section of the holotype, enlarged from in fig. 7, showing seed shriveled inside the locule, and vascular bundle distal from the septum (arrow). RL, ×20.

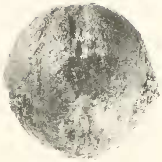
14. Same specimen, transversely sectioned closer to the apex, showing single layer of cuboidal cells surrounding the locules and forming zones of weakness along the planes of dehiscence (arrows). RL, ×30.

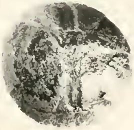
15. Peel from specimen in fig. 8, showing thick layer of isodiametric sclereids comprising the endocarp. TL, ×60.

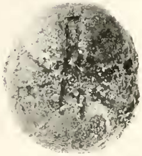

1


2


3

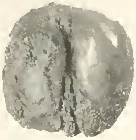

4

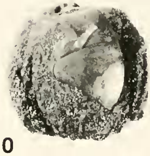

5

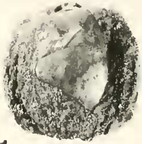

6

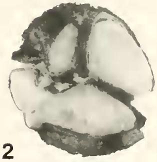

7


8


9

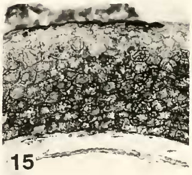

10


11


12

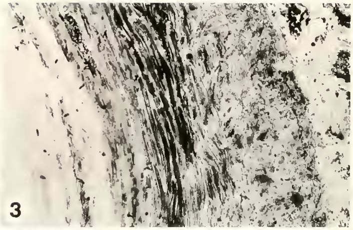

13


14


15


1


2


3


4


5


6


7


8


9

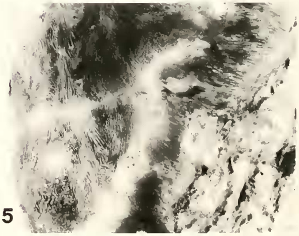

10


11


12


13


14


15

EXPLANATION OF PLATE 10

Figure Page

1–3. *Mastixia* sp. 42

1. Transverse section of an endocarp with adhering matrix, showing smooth outer wall and outline of seed coat within the locule. UF 6502. Etched, RL, ×6.5.
2. Transverse section of an endocarp in matrix showing typical thick dorsal infold and lines of dehiscence. UF 6303. RL, ×6.5.
3. Transverse peel of endocarp wall, showing inner layer of horizontally aligned fibers, and an outer layer of obliquely aligned fibers. UF 6502. TL, ×30.

4–11. *Mastixioidiocarpum oregonense* Scott. 43

4. Transversely fractured fruit in matrix, showing prominently sculptured surface of endocarp and relatively narrow dorsal infold. UF 9207. RL, ×3.
5. Transverse section of fruit in matrix, with the surface sculpture worn by erosion, showing narrow dorsal infold, and a pair of lacunar canals adjacent to the lines of dehiscence. UF 9269. RL, ×5.5.
6. Same, detail of wall, with lacunar canal. RL, ×15.
7. Same, showing swirling tracts of fibers. RL, ×30.
8. Latex cast prepared from the sedimentary mold of an endocarp, showing rough external sculpture and ovoid shape. UF 9206. ×2.5.

9–11. Fossil boat-shaped locule cast recovered from the mold of the specimen in fig. 8. ×3.5.

9. Lateral view showing smooth surface, pointed apex, rounded base.
10. Ventral view showing the convex surface.
11. Dorsal view showing the median groove.

12–15. *Mastixicarpum occidentale* sp. nov. 44

12. Fruit in matrix, broken and revealing elongate, boat-shaped locule cast. UCMP 10705. RL, ×2.5.
13. Transverse section of the same specimen showing thick wall including epicarp with smooth surface. Note seed within the locule and line of the dehiscence plane within the endocarp (arrow). RL, ×3.
14. Fruit in transverse section showing slight separation of epicarp from the endocarp, particularly apparent at lower left. Holotype, UF 8740. RL, ×3.
15. Same, detail showing swirling tracts of fibers in the endocarp and anticlinally oriented fibers of the epicarp. Note secretory canals in outer layer. RL, ×15.

EXPLANATION OF PLATE 11

Figure Page

1–10. *Langtonia bisulcata* Reid et Chandler. 44

1. Complete endocarp in matrix, longitudinal view. UF 8731. ×2.
2. Broken endocarp with the two locule casts protruding, longitudinal view. UF 8734. ×2.
3. Apical view of the same specimen. ×2.
4. Etched transverse section of the endocarp from fig. 1, with one of the locules abortive. ×2.
5. Isolated locule cast, ventral view, showing elongate, convex ellipsoidal outline and the median longitudinal raphe. UF 8738. ×2.5.
6. Same, dorsal view, showing pair of grooves corresponding to infolds of the endocarp. ×2.5.
7. Transverse section of a typical endocarp showing thick wall, two fully developed w-shaped locules, and faint lines delimiting the germination valves (arrows). UF 8730. ×2.5.
8. Transverse section of a small fruit with one fully developed locule. Note the epicarp preserved as a dark layer surrounding the endocarp; dorsal infolds (arrows) can be seen corresponding to an abortive locule, as well as those corresponding to the fully developed locule. USNM 424875. ×2.5.
9. Acetate peel from fig. 8, magnified to show fibers making up the endocarp and remains of a seed within the underdeveloped locule. USNM 424875. TL, ×30.
10. Acetate peel from specimen in fig. 8, showing endocarp made up of variously oriented fibers, intruded and surrounded by the epicarp of thin-walled cells. Secretory canals present in the epicarp (arrows). TL, ×30.

11–19. *Nyssa spatulata* (Scott) comb. nov. 45

11. Complete endocarp in matrix, longitudinal view showing ellipsoidal outline and equatorial plane of transverse section in fig. 16. UF 6842. ×1.8.
12. Abraded endocarp showing elliptical outline of germination valve. USNM 40543. ×2.5.

13–15. Isolated locule cast. UF 6838. ×2.5.
    13. Ventral surface, showing obovate outline.
    14. Dorsal surface.
    15. Lateral view, showing curvature, ventral surface to the left.

16. Transverse section of fig. 11, showing three c-shaped locules, thick wall and undulate margins of the endocarp. ×2.0.
17. Apical view of fig. 12, showing the outline of 3 protruding locules casts delimiting three germination valves. ×2.5.
18. Transverse section of a complete endocarp preserved in matrix. UF 6837. RL, ×2.5.
19. Anatomical detail of endocarp from section in fig. 18, showing masses of fibers oriented in different directions. TL, ×50.


1

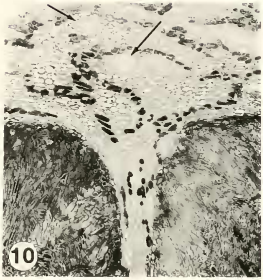

2


3


5


6


4


10


7


8


9


11

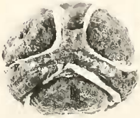

12

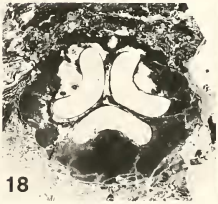

13

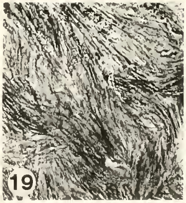

14


15

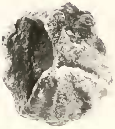

16


17


18

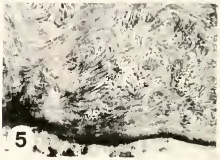

19


1


2

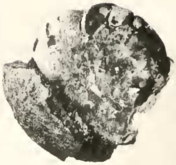

3


4

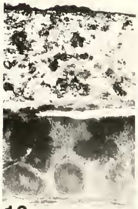

5

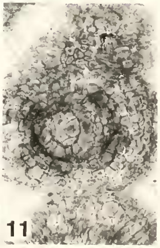

6

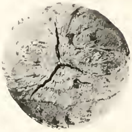

7

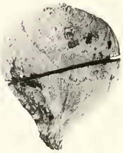

8


9


10


11


12


13


14


15


16


17


18

EXPLANATION OF PLATE 12

Figure Page

1, 2. *Nyssa scottii* sp. nov. 46
- 1. Chalcedony endocarp cast, lateral view, with one of the germination valves removed. Holotype, USNM 354588. PC, ×4.5.
- 2. Same, apical view, showing the three germination valves, the one on the left broken away. PC, ×4.5.

3–5. *Nyssa* sp. 46
- 3. Large unilocular endocarp, lateral view, showing rounded apex and longitudinal surface grooves. UF 9757. ×1.5.
- 4. Same, sectioned transversely, showing thick endocarp wall and single locule. RL, ×1.5.
- 5. Same, detail of endocarp wall showing swirling tracts of fibers. RL, ×30.

6–11. *Castanopsis crepetii* sp. nov. Holotype, UF 9267. 46
- 6. Complete fruit including cupule, viewed basally, showing circular outline. ×1.25.
- 7. Same, viewed laterally, with portions of wall broken away revealing locule cast which is pointed apically and truncate basally. ×1.25.
- 8. Same, basal view, showing undulating circular outline of locule cast. ×1.25.
- 9. Transverse section of the wall from fig. 6, showing dark endocarp layer surrounded by the adnate cupule. RL, ×2.
- 10. Detail of tranverse section, showing relatively dense tissue of the nutshell (lower half of photo), and less compact tissue of the cupule (upper half of photo). Note islands of concentrically arranged fibers in the nutshell. RL, ×12.5.
- 11. Same, detail of nutshell, showing concentrically arranged fibers. TL, ×75.

12–15. Extant *Castanopsis piriformis* Hick. et A. Camus. Vietnam. M. Poilane 30313 (US 2493106). 47
- 12. Apical view, showing relatively smooth circular outline, for comparison with fig. 6. ×1.25.
- 13. Lateral view, showing saw cut for transverse section in fig. 14. ×1.25.
- 14. Transverse section of the wall, showing nut surrounded by adnate cupule; cf. fig. 9. RL, ×2.
- 15. Same, thin section of the nutshell, showing islands of concentrically arranged fibers and an adjacent duct with dark contents; cf. fig. 11. TL, ×75.

16–18. *Quercus paleocarpa* Manchester. 47
- 16. Acorn, lateral view with nut and abraded cupule. Holotype, OMSI Pb176. ×1.25.
- 17. Same, apical view showing circular outline of the nut. ×1.25.
- 18. Isolated cupule in matrix, lateral view, showing concentric transverse ribs. USNM 414508. ×2.

EXPLANATION OF PLATE 13

Figure		Page
1–16.	*Saxifragispermum tetragonalis* sp. nov.	48

1. A complete fruit viewed laterally showing the smooth surface, more or less rounded base and pointed apex. UF 6471. ×4.2.
2. A similar fruit with some of the outer layer flaked away, revealing median longitudinal placental band. UF 6474. PC, ×4.
3. A fruit with some of the wall removed in the apical half, exposing two rows of seeds attached to adjacent longitudinal placental bands. UF 6477. ×4.

4, 5. Stereo-pair of a specimen with large portion of outer wall broken away revealing numerous seeds. Holotype, UF 5236. ×4.

6. Base of the specimen shown in fig. 2, showing four-fold symmetry, and four circular apertures corresponding to the placental bundles. PC, ×5.
7. Specimen from fig. 1, sectioned transversely, showing the medial position of the placenta on each of the four valves of the fruit (arrows). Some of the seeds are preserved showing thin seed coat. Etched, RL, ×8.
8. Transversely sectioned fruit in siltstone matrix, showing four parietal placentae with attached seeds. USNM 354008. RL, ×8.
9. Same, enlarged more, showing arrangement of seeds around the placenta and pair of vascular bundles within the placenta. RL, ×25.
10. Detail from fig. 5, showing ovoid seeds in attachment to the placenta. Subsequent transverse sectioning revealed that the row of seeds on the left are borne on the placenta to the left, while the row on the right corresponds to another placenta. SEM, ×8.5.
11. Longitudinally fractured fruit, showing dense mass of tortuous, more or less longitudinal, fibers and the impression of several seeds. UF 6575. SEM, ×20.
12. Same, showing a seed fractured along the inside of the seed coat showing horizontally elongate hexagonal cells surrounded by fibers of the pericarp. SEM, ×155.
13. Outer surface of a seed surrounded by fibers of the pericarp. SEM, ×85.
14. Finer detail of same, showing the rectangular outline of seed coat cells. SEM, ×400.
15. Detail from fig. 7, showing two seeds (arrows). Seed on right shows rectangular cells of seed coat. RL, ×120.
16. Seed from section in fig. 7, showing peripheral trichomes and shriveled inner layer of seed coat. RL, ×140.

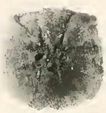

1

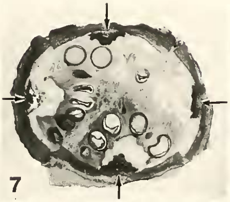

2


3


4


5


6


7


8


9

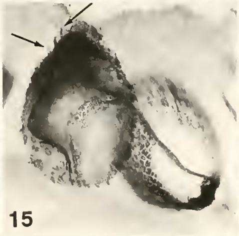

10


11


12

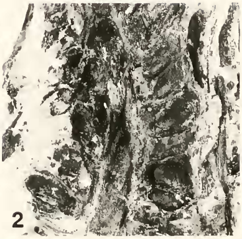

13


14

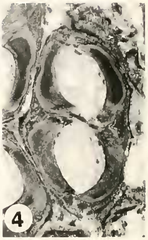

15


16


1


2


3


4


5


6


7


8


9


10


11


12


13


14


15


16

Explanation of Plate 14

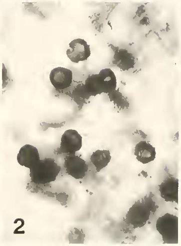
Figure Page

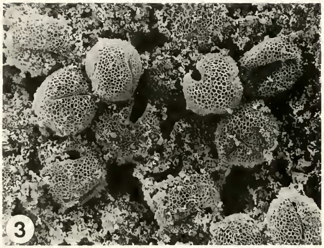
1–13. *Fortunearites endressii* gen. et sp. nov. 49
- 1–5. Permineralized infructescence. Holotype, OMSI Pb156. (Counterpart of USNM 354581).
    - 1. Infructescence fractured longitudinally. OMSI Pb156. RL, ×1.5.
    - 2. Counterpart, showing stout axis and longitudinally fractured bilocular fruits. USNM 354581. RL, ×2.
    - 3. Tangential section of the axis in fig. 2 showing the bilocular capsules in transverse view. RL, ×3.
    - 4. Same, showing thin septum between locules and thick endocarp wall. RL, ×5.
    - 5. Transverse section of the axis in fig. 2, showing radiating fruits. RL, ×2.5.
- 6. Paired locule casts from a single fruit, face view. UF 9258. PC, ×6.
- 7. Same, apical view of the locule casts, cf. fig 4. PC, ×6.
- 8. Isolated locule cast removed from the infructescence in fig. 2, lateral view. USNM 354581. PC, ×8.
- 9. Same, ventral view. PC, ×8.
- 10–11. Stereo-pair, internal mold of seed coat, face view, showing band of the raphe traveling along the lower 3/4 of seed periphery. USNM 424651. PC, ×8.
- 12. Same, basal view, with the raphe offset toward one side. PC, ×8.
- 13. Same, rotated 90° from fig. 11. PC, ×6.

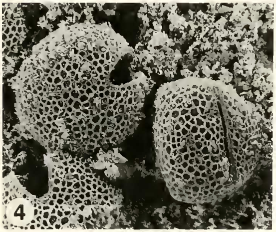
14–16. Staminate hamamelidaceous inflorescence. UF 5567. 50
- 14. Medial section through inflorescence in siltstone matrix, showing at least seven florets in oblique-lateral view. Each floret set off by perianth and containing conspicuous stamens. Etched, RL, ×7.
- 15. An individual floret from the same inflorescence sectioned transversely near the apex showing five anthers with interspersed small staminodes surrounding clumps of pistillode hairs. Etched, RL, ×14.
- 16. Same, sepal in transverse section showing stellate trichomes on the abaxial (left) surface and and simple trichomes on the adaxial (right) surface. TL, ×65.

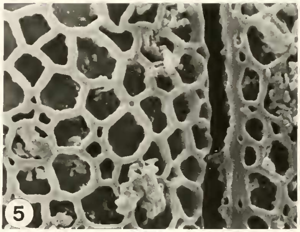
EXPLANATION OF PLATE 15

Figure		Page
1–5.	Staminate hamamelidaceous inflorescence, continued. UF 5567	50
1.	Anther in transverse section from the floret in Pl. 14, fig. 15, showing pollen within the locules. Thin section, RL, ×60.	
2.	Same, enlargement showing globose tricolpate pollen grains preserved within translucent silica. TL, ×250.	
3.	Tricolpate reticulate pollen in situ within an anther. Etched, SEM, ×750	
4.	Polar and equatorial views of the pollen, showing reticulate ornamentation and elongate colpi. Etched, SEM, ×1500	
5.	Detail of exine showing smooth wall of the aperture and columellae beneath the reticulate tectum. SEM, ×7500.	
6.	*Hydrangea* sp. sterile flower from Gonser Road Clarno locality 238. UF 9962.	51
7, 8.	*Hydrangea knowltonii* sp. nov.	50
7.	Fruiting panicle from the Nut Beds showing apparent trifurcate branching and numerous capsules. OMSI Pb697. ×2.	
8.	Counterpart of same, enlarged to show capsule with two styles, thickened apical disk and longitudinal striations. ×8.	
9.	Extant *Hydrangea arborescens* L. Fruiting panicle with persistent fertile flower. Fruits showing longitudinal striations, thickened apical disks and two styles each. Summit Lookout Mountain, Tennessee. A. Cuthbert, Sept. 16, 1908 (FLAS 9652). ×2.	51





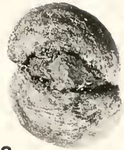





9


1


2


3


4


5


6


7


8


9


10


11


12


13


14


15


16

EXPLANATION OF PLATE 16

Figure Page

1–15. *Hydrangea knowltonii* sp. nov. 50

1. Tricarpellate capsule, apical view, showing triangular cast of dehiscence opening. Holotype, UF 6445. SEM, ×8.
2. Tricarpellate capsule, basal view, UCMP 10669. ×8.
3. Bicarpellate capsule, basal view, showing wedge-shaped cast of dehiscence opening. UF 6444. ×10.
4. Same, basal view, showing thickness of septum. PC, ×10.
5. Same, lateral view, showing apical wedge where the capsule was splitting. PC, ×10.
6. Lateral view of the holotype, cf. fig. 1, showing transverse striations. ×8.
7. Basal view of a bicarpellate specimen. Note fingerprint pattern of fine transversely oriented striations. UF 8696. ×8.
8. Same, sectioned transversely, showing pair of deeply intruded parietal placentae. Etched, RL, ×10.
9. Same, prior to sectioning, lateral view, showing transverse fibers of the endocarp and remains of the mesocarp composed of small polygonal cells and longitudinal fiber bands (arrows). UF 8696. SEM, ×15.
10. Transverse acetate peel section of the tricarpellate specimen in fig. 2, showing deeply intruded, parietal placentae and scattered dislodged seeds (arrows). UCMP 10669. TL, ×10.
11. Transverse section of a bicarpellate fruit, showing single locule with deeply intruded, parietal placentae and loose seeds. UF 6446. Etched, TL, ×10.
12. Thin section of a fruit showing three seeds. UF 9385. RL and TL, ×50.
13. Thin section of the same fruit showing seeds with embryo in cross section. RL and TL, ×50.

14, 15. Isolated seeds from fruit dissolved in hydrofluoric acid. UF 9883. TL, ×50.

16. Extant *Hydrangea anomala* D. Don. Seed showing stout hilum, elliptical central body and surrounding wing for comparison with figs. 14, 15. Ishikari Province, Japan. K. Miyabe (Mo 3838165). RL and TL, ×30. 51

EXPLANATION OF PLATE 17

Figure		Page
1–8.	*Iodes multireticulata* Reid et Chandler.	51
1.	Chalcedony endocarp cast, face view, showing areolate pattern of surface ridges and more or less elliptical outline, UCMP 10702. PC, ×5.	
2.	Apical view of same, showing median keel with a raised trough (arrow) representing the funicle. PC, ×5.	
3, 4.	Stereo-pair of endocarp mold in siltstone, face view, showing the characteristic reticulum of surface ridges with funicle following fruit contour (arrow). UF 6458. ×5.	
5.	Chalcedony locule cast from the same specimen as in figs. 3, 4, face view, showing reticulate surface, median longitudinal groove representing path of the raphe, running between the hilum (h) and chalaza (c). PC, ×5.	
6.	Same, apical view, showing relatively narrow outline and keel in plane of bisymmetry. PC, ×5.	
7.	Same, enlarged to show punctate locule cast surface. SEM, ×20.	
8.	Detail of same, showing rows of circular punctae representing papillae of the locule lining. SEM, ×280.	
9–16.	*Iodes chandlerae* sp. nov.	53
9.	Chalcedony locule cast with very faint surface reticulations. The locule cast is partially broken to show the smooth seed cast inside. Note median groove of the raphe (r). Holotype, USNM 424743. PC, ×5.	
10.	Same, basal view showing smooth contour of the seed, the circular chalaza (c), and groove of the raphe (r). PC, ×5.	
11.	Same, detail of locule cast surface, showing characteristic punctae. SEM, ×100.	
12.	Same, detail of seed cast surface, showing rows of rectangular cells. SEM, ×100.	
13.	Locule cast, face view, showing truncate base and asymetrical apex with weak median ridge and very faint reticulum. USNM 422383. PC, ×5.5.	
14.	Same, lateral view, showing pointed apex, truncate base and longitudinal keel in plane of bisymmetry. PC, ×5.5.	
15, 16.	Same, basal view, showing the intersection of ridges forming a cross pattern. PC, ×5.5.	


1

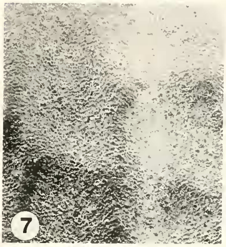

2


3


4

5


6

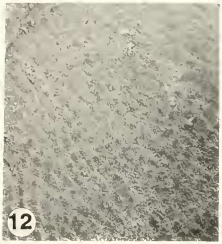

7


8

9

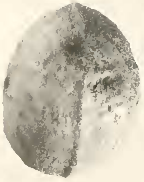
10


11


12


13


14


15


16


1


2


3

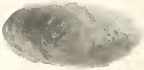

4


5


6


7

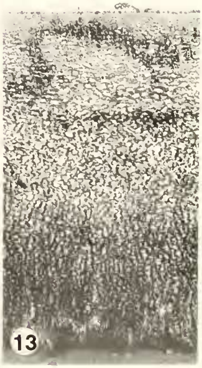

8


9


10


11


12


13


14

EXPLANATION OF PLATE 18

Figure — Page

1–6. *Iodicarpa ampla* gen. et sp. nov. × 1.25. . . . 53

1. Endocarp, face view, showing longitudinally rugulate and verrucate surface. Holotype, USNM 354788. PC.
2. Somewhat abraded specimen, face view, showing rough, longitudinally ribbed surface. USNM 354789.
3. Mold of an endocarp in siltstone matrix, showing veinlike reticulum. USNM 446085.
4. Endocarp, face view, showing showing reticulate pattern of surface grooves. UF 8618. PC.
5. Holotype as in fig. 1, apical view, showing roughly lensoidal outline.
6. Transverse section of specimen in fig. 2, showing elliptical outline of locule, horizontal plane of dehiscence, and funicular canal (arrow).

7–10. *Iodicarpa lenticularis* sp. nov. × 1. . . . 54

7. Endocarp, face view, showing elliptical outline and relatively smooth surface. Holotype, USNM 354816.
8. Smaller specimen, face view. USNM 354796.
9. Apical view of specimen in fig. 7, showing lensoidal outline and course of funicle along the right margin.
10. Same, transverse section showing thickness of wall and outline of locule, partially filled with chalcedony and quartz crystals. × 1.

11. *Iodicarpa ampla* sp. nov. Transverse section of specimen in figs. 2, 6, showing pappilate locule lining (above) and elongate, sinuous-walled cells of the endocarp. L, × 30. . . . 53

12–14. *Iodicarpa lenticularis* sp. nov., details of anatomy. . . . 54

12. Transverse section of holotype, figs. 7, 9, 10, showing papillate locule lining (above) and sinuous-walled cells with intracellular spaces of the endocarp. TL, × 75.
13. Transverse section of the specimen in fig. 8, showing papillate locule (above), and full thickness of endocarp with tissue grading from more or less horizontally aligned cells near the locule to vertically aligned cells distally. TL, × 30.
14. Same, showing thin seed coat, papillae of the locule lining and intracellular spaces within the endocarp tissue. TL, × 75.

EXPLANATION OF PLATE 19

Figure — Page

1–9. *Comicilabium atkinsii* gen. et sp. nov. — 55
  1. Endocarp, apical view showing funicular bulge. Holotype, USNM 354783. PC, ×1.8.
  2. Same, ventral view, showing longitudinal groove leading to the funicular bulge. PC, ×1.8.
  3. Same, basal view showing radiating meridional grooves. PC, ×1.8.
  4. Somewhat abraded endocarp, apical view showing the transverse funicular slit; source of sections in figs. 7, 9. USNM 446084. ×1.5.
  5. Holotype as in figs. 1–3, lateral view showing longitudinal grooves and the apical funicular bulge. PC, ×1.5.
  6. Dorsal view of an endocarp showing longitudinal groove in plane of bisymmetry, and apical funicular bulge. UF 8596. PC, ×1.5.
  7. Same specimen as in fig. 4, sectioned transversely, showing thickness of endocarp wall, and the seed with two thick cotyledons. RL, ×2.
  8. Transverse thin section of the specimen in fig. 6, showing thickness of endocarp wall. RL, ×10.
  9. Detail from fig. 7, showing balloon-like papillae lining the locule. RL, ×185.

10–14. *Pyrenacantha occidentalis* sp. nov. — 57
  10. Endocarp, face view, showing ovate outline and punctate exterior. Holotype, UCMP 10708. ×1.5.
  11. Same, basal view. ×1.5.
  12. Same, sectioned transversely, showing thin endocarp wall and elongate endocarp projections into the locule. RL, ×1.5.
  13. Same, magnified to show tubular structure of the endocarp projections. RL, ×7.
  14. Same, anatomy of endocarp projection showing elongate, undulate-walled cells. RL, ×20.

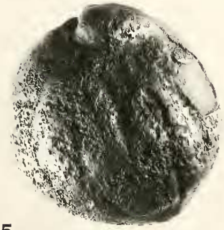
15–18. Extant icacinaceous fruits. — 51–57
  15. *Pyrenacantha zenkeri* (sp. Moore) Exell. Transverse section of fruit showing thin endocarp wall with elongate protrusions into the locule. Angola. Gossweiler 8730 (BARC). RL, ×4.
  16. *Phytocrene macrophylla* (Bl.) Bl. var. *macrophylla* (det. H. Sleumer). Endocarp with typical surface pitting. Leyte Island, Philippines, January 1906. A.D.E. Elmer 7134 (A). ×0.9.
  17. *Phytocrene oblonga* Wall. Transverse section showing pits of the endocarp without protrusions into the locule. "Austro Cohui Chinae". L. Pierre 2837 (A). ×2.5.
  18. *Iodes cirrhosa* Turcz. Papillate lining of the locule. Perak, Ipoh, Malaya. S.C. Chin 994 (L 401157). SEM, ×27.5.


1


2


3


4


5


6


7


8

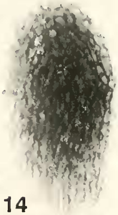

9


10


11


12

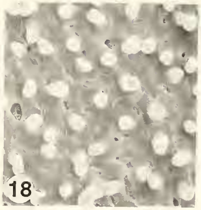

13

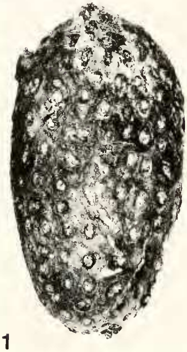

14


15


16


17


18



1

2

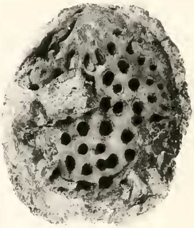
3

4

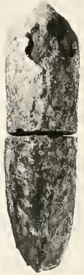
5

6

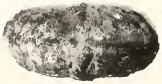
7



8



9



10

11

12

13

EXPLANATION OF PLATE 20

Figure Page

1–5. *Palaeophytocrene hancockii* Scott. 56

1. Locule cast, face view view showing prominent pits and obovate outline. USNM 312751. × 1.
2. Same, lateral view, showing thickness and narrowed apex. × 1.
3. Transverse section of permineralized endocarp; some of the wall has broken away from the locule cast. Note thickness of wall, hollow protrusions into the locule, and shriveled seed coat. UF 9567. RL, × 1.25.
4. The same, magnified to show detail of endocarp wall including a protrusion into the locule. RL, × 7.5.
5. Anatomy of the endocarp showing interdigitating cells and tiny papillae lining the locule (top of figure). UF 9567. RL, × 60.

6–13. *Palaeophytocrene pseudopersica* Scott. 56

6. Endocarp, face view, with pitting indistinct at the surface, prior to sectioning (figs. 9, 11). UF 8597. × 1.5.
7. Endocarp with part of the outer layer broken away revealing numerous pits. UF 8608. × 1.5.
8. Locule cast with adhering remains of the endocarp. OMSI Pb181. × 1.5.
9. Same specimen as in fig. 6, lateral view, showing thin profile (contrast with fig. 2), and position of transverse section shown in fig. 11. × 1.5.
10. Same, basal view, showing cross-shaped intersection of longitudinal ribs. × 1.5.
11. Same, transverse section showing relatively thick wall, hollow protrusions of endocarp into locule, and collapsed seed coat. × 2.5.
12. Locule cast, face view, showing prominent pits and wide, nearly circular, outline. UF 8599. × 1.5.
13. Same, lateral view, showing thickness and apical keel. × 1.5.

EXPLANATION OF PLATE 21

Figure Page

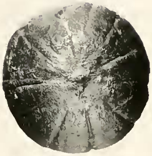
1–9. *Juglans clarnensis* Scott. 58

1. Chalcedony nut cast, lateral view, showing smooth elliptical outline, small apical projection and meridional grooves. UF 5338. PC, ×1.5.
2. Same specimen, apical view, showing smooth circular outline with about 12 meridional grooves. PC, ×1.5.
3. Nut opened along the plane of dehiscence showing thick wall, and the locule with two prominent cavities corresponding to the two cotyledons. UF 4872. ×2.
4. Permineralized nut, transverse section showing two lobes of the locule, two distinct placental bundles in the primary septum, and four flattened lacunae in the nut wall. UF 7965. RL, ×2.5.
5. Chalcedony locule cast, lateral view showing extent of primary septum. UF 9461. ×2.
6. Same, rotated 90°, showing straight shoulder regions, median line of dehiscence and rounded base of lobes without development of a secondary septum. ×2.
7. Chalcedony locule cast in lateral view showing position and extent of primary septum, and two cotyledon lobes. UF 9458. ×2.
8. Same, rotated 90°, indicating weak formation of a secondary septum. ×2.
9. Same, viewed apically, orientation the same as specimen in fig. 4. ×2.

10–17. *Cruciptera simsonii* (Brown) Manchester. 57

10. Transversely compressed samara viewed apically showing four elongate wings radiating from a circular nutlet. OMSI Pb1580. ×1.5.
11. Smaller specimen with well-preserved nutlet as seen in fig. 14. UF 9612. ×2.
12. Longitudinally fractured specimen showing elongate pedicel (p) and the wings arising equatorially from the nutlet. OMSI Pb899. ×4.
13. Detail of wing showing subparallel, thin dichotomizing venation. OMSI Pb776. ×5.
14. Detail of nutlet from the samara in fig. 11, sectioned transversely showing plane of dehiscence, oriented vertically, and three lobes of the locule; a fourth locule lobe, upper right, is not preserved but may be inferred from the symmetry. RL, ×10.
15. Transverse section in the basal one-third of an isolated silicified nutlet showing four lobes of the locule, delimited by thick primary horizontal and secondary vertical septa. UF 8867. RL, ×8.
16. Same, sectioned closer to the equator, near the top of the secondary septum, with the four basal lobes of the locule joining to form two lobes. Note lacunae in the wall at both sides of the primary septum. RL, ×8.
17. Chalcedony locule cast showing basal cleavage from the primary and secondary septa. USNM 354375. SEM, ×10.


1

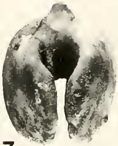

2


3


4


5


6


7


8

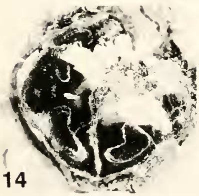

9

10


11

12


13


14


15

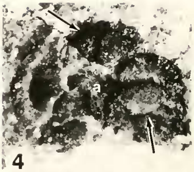

16


17


1


2


3


4


5


6

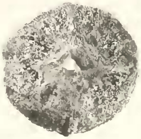

7


8


9


10


11


12


13


14


15


16


17

EXPLANATION OF PLATE 22

Figure Page

1–8. *Paleoplatycarya*? hickeyi sp. nov. . . . 60

1. Infructescence after dispersal of fruits, lower half showing natural longitudinal fracture, upper half sectioned longitudinally, revealing broadly triangular helically arranged bracts. UF 9251. ×3.

2, 3. Stereo-pair, longitudinally fractured permineralized infructescence, showing stout axis and intact locule casts (arrows). Holotype, UF 6454. ×5.

4. Same infructescence fractured transversely, showing two bilobed locule casts (arrows) arranged around the central axis (a). ×7.5.

5. Locule cast removed from the same infructescence, showing prominent groove of the primary septum, rounded base of lobes and pointed apex. SEM, ×16.

6. Isolated locule cast, face view, showing cleft from primary septum. UF 8763. SEM, ×20.

7. Same as fig. 5, apical view, showing narrow dorsiventral thickness. SEM, ×15.

8. Same, basal view. SEM, ×16.

9–17. Cf. *Palaeocarya clarnensis* Manchester. . . . 59

9. Isolated locule cast. UF 8756. SEM, ×15.

10. Permineralized nut, lateral view, with part of the nutshell fractured away, revealing the locule cast with a median cleavage corresponding to the septum. USNM 424640. PC, ×10.

11. Same, rotated 90°, showing acute base and median longitudinal rib. PC, ×10.

12. Same, apical view, showing rounded outline and single longitudinal rib (lower part of figure). PC, ×10.

13. Same specimen, sectioned transversely near the equator showing thin fruit wall, incomplete primary septum and shriveled seed within the bilobed locule. RL, ×15.

14. Nut, lateral view, showing elongate-conical base of nut. Nutshell broken away in upper half, revealing the rounded, apically pointed locule cast. Note the prominent median longitudinal rib. UF 9361. SEM, ×10.

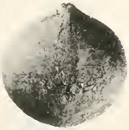
15. Chalcedony locule cast showing smooth contour and median line of dehiscence. Note absence of secondary septum development. UF 8752. SEM, ×12.

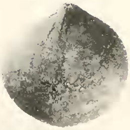
16. Same, apical view, showing plane of dehiscence (vertical) and septum (horizontal). SEM, ×12.

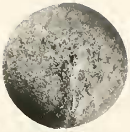
17. Nut sectioned transversely near the equator, showing endocarp with line of dehiscence and septum. USNM 458416. RL, ×15.

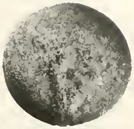
EXPLANATION OF PLATE 23

Figure		Page
1–8.	*Lindera clarnensis* sp. nov.	61
1, 2.	Stereo-pair, ventral view, showing globose shape and faint ridge running from the equator to the apex. USNM 424728. PC, ×7.5.	
2, 4.	Same, stereo-pair, apical view, showing circular outline and ventral ridge. PC, ×7.5.	
5.	Same, sectioned transversely, showing thin testa and vertical line separating the large planoconvex cotyledons. RL, ×10.	
6.	Specimen, with remains of endocarp adhering to locule cast. Holotype, USNM 435006 PC, ×5.	
7.	Same, enlarged to show columnar cells of the endocarp. SEM, ×50.	
8.	Same, detail of columnar cells. SEM, ×100.	
9–15.	*Laurocalyx wheelerae* sp. nov.	61
9.	Endocarp, basal view, showing circular outline, smooth surface and prominent attachment scar. USNM 424807. PC, ×3.	
10.	Same, lateral view, showing height nearly equal to width, truncation at the attachment scar. PC, ×3.	
11.	Endocarp dislodged from its cupule (fig. 13), basal view showing elliptical attachment scar. Holotype, UF 9406. PC, ×3.	
12.	Same, lateral view, showing relatively short length. PC, ×3.	
13.	Same, in matrix with basally attached cupule, longitudinal section. RL, ×4.	
14.	Same, enlargement of cupule tissue, showing frequent oil cells with contents preserved as dark spots, and showing the contact of the cupule with the base of the fruit. RL, ×25.	
15.	Same, detail of transition between cupule (c) and seed (s). Note the uniseriate layer of dark columnar cells of the endocarp (arrow). RL ×50.	


1


2


3

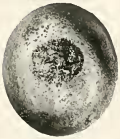

4

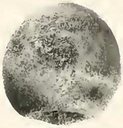

5


6

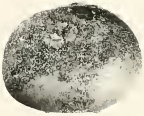

7


8


9


10


11


12

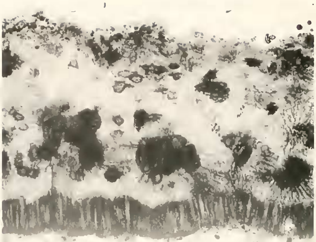

13


14


15


1


2

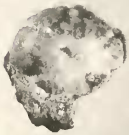

3

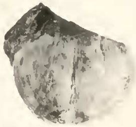

4


5

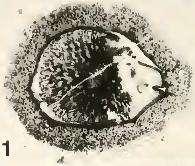

6

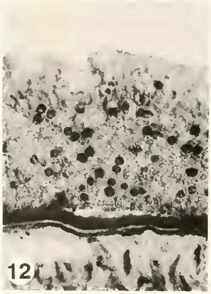

7

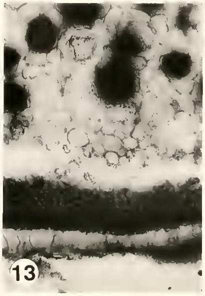

8

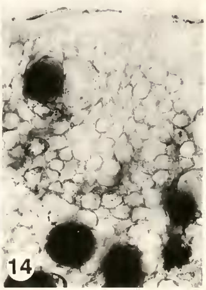

9

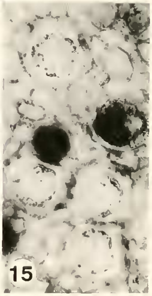

10


11


12


13


14


15

EXPLANATION OF PLATE 24

Figure | Page

1–3. *Laurocarpum hancockii* sp. nov. Holotype, OMSI Pb262. . . . 62

1. Lateral view of specimen with adhering siltstone matrix, partially broken showing thickness of wall surrounding locule cast. ×2.
2. Transverse section showing circular outline, unilocular with shriveled remains of the seed. ×2.
3. Fruit wall showing columnar layer lining the locule and outer parenchymatous layer with stone cells. ×30.

4–7. *Laurocarpum nutbedensis* sp. nov. Holotype, USNM 435090. 62

4. Lateral view showing more or less elliptical outline and smooth surface. The base is incomplete. PC, ×5.
5. Transverse section showing circular outline, thick endocarp wall and remains of two large cotyledons that filled the seed cavity. RL, ×7.
6. Same, enlarged to show cells of the endocarp, locule lining and seed coat. RL, ×15.
7. Same, acetate peel, showing endocarp composed of parenchyma with occasional interspersed larger, more rounded oil cells, and junction with seed coat. TL, ×50.

8–15. *Laurocarpum raisinoides* sp. nov. Holotype, UF 5672. 62

8. Basal view, showing central attachment scar, some adhering siltstone on the lower left. ×5.
9. Lateral view, showing fine longitudinal grooves. ×5.
10. Same, showing transverse plane of section used for fig. 11. ×5.
11. Transverse section, showing thick wall and unilocular, single-seeded construction. RL, ×8.
12. Detail from transverse section, showing numerous oil cells with dark contents scattered through the mesocarp. RL, ×50.
13. Detail of wall layers adjacent to the locule (lower part of figure). Note locule lining of uniseriate thin-walled columnar cells, next a 5–8-seriate layer of sclereids, followed by a tissue of large parenchyma cells with occasional interspersed oil cells. RL, ×200.
14. Same, showing exocarp of columnar cells exterior to the mesocarp tissue of parenchyma cells with interspersed oil cells. RL, ×200.
15. Mesocarp tissue showing several closely spaced oil cells. RL, ×270.

EXPLANATION OF PLATE 25

Figure Page

1–8. *Decodon* sp. 63

1. Fruit with numerous seeds in siltstone. UF 5675. ×8.
2. Same, transverse section showing seeds in various orientations. RL, ×10.
3. Isolated permineralized fruit, transversely broken. UF 5668. ×15.
4. Same, transverse section, showing angular to rounded seeds with white embryo casts. RL, ×20.
5. Longitudinal section showing persistent pedicel, hypogynous calyx (c), longitudinal septation (s) and radiating seeds. UF 6449. RL, ×10.
6. Detail from fig. 4, showing several seeds intercepted at levels showing the enlarged columnar cells of the germination valve (v). RL, ×40.
7. Transverse section of a seed from the specimen in figs. 1, 2, showing the embryo cavity (e), and the ventrally thick layer of isodiametric cells through which the raphe (r) passes. RL, ×50.
8. Transverse section of another seed in the same fruit. UF 5675. RL, ×50.

9. *Leguminocarpon* sp. OMSI Pb1725. ×1.5. 63

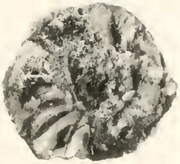
10–12. *Magnolia tiffneyi* sp. nov., chalcedony seed cast. Holotype, UF 6549. PC, ×6. 65

10. Ventral view, showing median raphe groove and deep cleft at heteropyle with protruding stalk.

11, 12. Dorsal view showing V-shaped moat with stalk extending longitudinally.


1


2


3


4

5

6

7


8


9


10


11


12

1

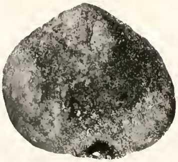
2

3

4

5

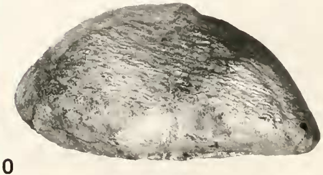
6



7

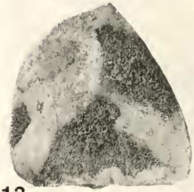
8

9



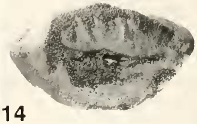
10

12

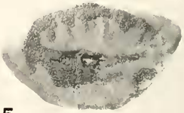


13

11



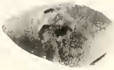
14



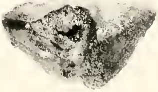
15

16

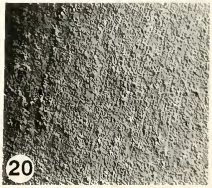
17



18



19



20

EXPLANATION OF PLATE 26

Figure Page

1–9. *Magnolia muldoonae* sp. nov. 64

1. Infructescence permineralized in sediment, transversely fractured showing thick woody folicles; note seed upper left. Holotype, UF 6529. ×3.
2. Same, transverse section with four folicles radiating from the central axis. ×3.

3–9. Chalcedony seed casts. PC, ×6.

3. Ventral view, showing ovate outline, pointed hilar end and median basal raphe groove. USNM 424698.
4. Dorsal view, showing concave heteropyle area. UF 6556.
5. Smaller specimen, ventral view, showing well preserved heteropyle. UF 6546.
6. Broader specimen, dorsal view, showing slight collar at the chalaza end. USNM 424697.

7, 8. Stereo-pair of same specimen, ventral view, showing slight swelling or collar surrounding a small moat and stalk. Viewed in stereo, the stalk is seen to extend ventrally in contrast to the straight stalk of other species (cf. Plate 25, figs. 11, 12).

9. Another specimen, dorsal view, showing faint collar at the base. UF 6555.

10–17. *Magnolia paroblonga* sp. nov., chalcedony seed casts. PC, ×4. 65

10. Dorsal view, relatively wide specimen. UF 9188. PC, ×6.
11. Same, basal view showing elongate chalazal groove. PC, ×6.

12, 13. Stereo-pair, narrower specimen showing pointed hilar end and truncate base. Holotype, UF 9192. PC, ×6.

14, 15. Same, stereo-pair, basal view showing elongate chalazal groove. PC, ×6.

16. Ventral view, with elongate chalaza groove at base and longitudinal striations. UF 9191. PC, ×4.
17. Same, basal view showing wide heteropyle groove. PC, ×4.
18. *Magnolia muldoonae* sp. nov. Basal view of the specimen in fig. 5. PC, ×6. 64
19. *Magnolia tiffneyi* sp. nov. Basal view of the specimen in Pl. 25, figs. 10–12. PC, ×6. 65
20. *Magnolia muldoonae* sp. nov. Striations on the surface of chalcedony seed cast from fig. 9. SEM, ×40. 64

EXPLANATION OF PLATE 27

Figure Page

1–7. *Anamirta leiocarpa* sp. nov. 66

- 1. Endocarp showing smooth surface, dorsal keel and basal pedicel scar. USNM 424641. PC, ×5.
- 2. Cross section of specimen in fig. 1, approximately equatorial, showing thick endocarp wall, central bilobed condyle surrounded by locule with remnants of seed coat. ×5.
- 3,4. Successive serial longitudinal sections separated by 2 mm. ×5.
  - 3. Longitudinal section intercepting lateral periphery of the bilobed condyle showing circular endocarp wall and locule outline. UF 8728.
  - 4. Longitudinal section closer to the medial plane, showing bilobed condyle, horseshoe shaped locule and remnants of seed coat (arrow).
- 5. Longitudinally fractured endocarp, showing cordate condyle with median septum and surrounding subhemispherical locule. Holotype, UF 8745. ×5.
- 6. Median longitudinal section of an endocarp in matrix, basal portion, showing sediment-filled apertures of the condyle. UF 6308. ×7.
- 7. Longitudinal section showing anatomy of pericarp, with fiber orientation grading from periclinal on the inner part of the endocarp to anticlinal on the outer 2/3 of the endocarp. Some parenchyma cells of the mesocarp are preserved, top of photo. UF 5712. TL, ×100.

8, 9. Extant *Anamirta cocculus* (L.) Wight & Arn. J.N. Gowanloch (BARC). ×4.5. 66

- 8. Fruit sectioned through the condyle, cf. fig. 3.
- 9. Fruit sectioned in medial plane, showing bilobed condyle, horseshoe-shaped locule and bumpy endocarp surface, cf figs. 4, 5.

10–20. *Chandlera lacunosa* Scott. 66

- 10. Endocarp with faint median line of dehiscence. USNM 354472. ×1.
- 11. Laterally fractured specimen showing locule surrounded by thick-walled endocarp with rounded lacunae. UF 9249. ×1.
- 12–14. Cast of the lacunae system in the endocarp. UF 6850. ×1.
  - 12. Ventral view, showing outline of the condyle, and four projections representing the apical and basal apertures.
  - 13. Dorsal view showing median cleavage corresponding to suture line of the endocarp wall.
  - 14. Lateral view showing reticulation of lacunae system.
- 15. Apical view showing medial dehiscence line and paired apical apertures opening to the system of lacunae. UF 9254. ×1.25.
- 16. Transversely fractured specimen, showing crescent-shaped locule, paired ventral condylar cavities and lacunae within the endocarp. USNM 354537. ×1.5.
- 17–20. Locule casts. PC, ×1.25.
  - 17. Ventral view showing longitudinal median keel and subapical placenta (arrow). UF 6844.
  - 18. Same, dorsal view, showing median keel, pointed apex and base.
  - 19. Ventral view of a larger locule cast showing pointed apex and base. UF 6845.
  - 20. Same, dorsal view showing faintly irregular surface.


1

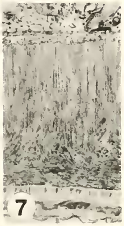

2

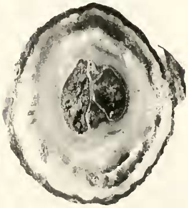

3


4


5


6


7




9


10


11


12


13


14


15


16


17

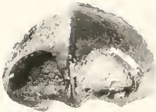

18

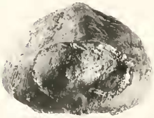

19


20


1


2


3


4


5


6

7

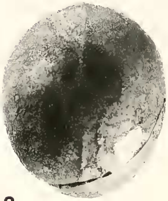
8


9

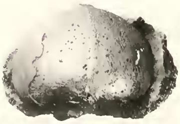

10


11


12


13


14


15


16


17


18

Explanation of Plate 28

Figure Page

1–10. *Odontocaryoidea nodulosa* Scott. 67

- 1–5. Chalcedony endocarp cast. USNM 424850. PC, ×2.5.
  - 1. Dorsal view, with median longitudinal keel and scabrate surface.
  - 2. Ventral view showing condylar cavity with faint transverse striations and median keel.
  - 3. Apical view showing the pair of cavities.
  - 4. Basal view showing bilobed cavity.
  - 5. Specimen with portion of endocarp broken away revealing thick wall and locule cast. UF 6869. ×3.
- 6–9. Chalcedony locule casts. PC, ×2.5.
  - 6. Dorsal view, showing median keel and flattened base. UF 6862.
  - 7. Ventral view of same, showing median keel, transverse striations and subapical placental scar (p).
  - 8. Lateral view. UF 6863.
  - 9. Same, ventral view, showing shorter length relative to fig. 7.
- 10. Endocarp in transverse section showing thick wall surrounding the crescent-shaped locule. UF 6873. RL, ×4.

11–17. *Calycocarpum crassicrustae* sp. nov. 69

- 11. Endocarp cast, dorsal view. USNM 424849. PC, ×2.5.
- 12. Same, ventral view of condyle cavity with median keel. PC, ×2.5.
- 13. Dorsal view of locule cast showing median keel. OMSI Pb471. PC, ×3.
- 14. The same, ventral, showing cup-shaped cavity and median keel. PC, ×3.
- 15. Apical portion of locule cast with some adhering endocarp. Holotype, UF 6769. PC, ×3.
- 16. The same, cross section, showing the thick endocarp surrounding the locule. RL, ×3.
- 17. Apical view of the specimen in figs. 13 and 14. PC, ×3.

18. Extant *Calycocarpum lyonii* (Pursh) Gray. Transverse section showing relatively thin endocarp wall. Locule similar to that in fig. 16. Florida. Curtis 5934 (A). ×3. 70

Explanation of Plate 29

Figure Page

1. *Calycocarpum crassicrustae* sp. nov. Transverse section of holotype illustrated in Pl. 28, figs. 15, 16, enlarged to show cells of the endocarp wall and testa. TL, ×60. 69

2–8. *Tinospora elongata* sp. nov. 70

2. Locule cast viewed dorsally, showing median keel and smooth surface. Holotype, USNM 354502. PC, ×4.8.

3, 4. Stereo pair of the same, viewed ventrally, showing condylar cavity, median keel, and a thin layer of adhering endocarp at the lower right. PC, ×4.8.

5. A larger locule cast, ventral. USNM 424648. PC, ×5.

6. Apical half of a broken locule cast. USNM 424649. PC, ×4.8.

7, 8. Stereo-pair of the same specimen, looking at the transversely broken end, showing the rounded condyle cast with a median groove representing the median keel of the ventral wall of the endocarp, surrounded by the c-shaped locule cast. The thin film between the locule cast and the condyle cast indicates that the endocarp was thin-walled. PC, ×4.8.

9–13. *Tinospora hardmanae* sp. nov. 70

9, 10. Stereo-pair of chalcedony locule cast, dorsal view, showing median keel and apical point, lower half of locule cast broken and removed, showing mold of ventral wall of the endocarp in sedimentary matrix. Holotype, UF 9255. ×6

11. Mold in siltstone matrix of the ventral surface of an endocarp, showing impression of the medial keel, supapical placenta and spines near the base. UF 9256. SEM, ×6.5.

12. Same, showing protrusion of endocarp spines into the matrix (arrows). SEM, ×10.

13. Chalcedony locule cast, ventral view, USNM 326715B. ×6.

14–16. *Eohypserpa scottii* sp. nov. 74

14. Sedimentary locule cast, lateral view, showing smooth circular outline, central plug and cleavage where the apex and base meet. USNM 446075. PC, ×4.

15. Locule cast viewed ventrally, showing median keel, and cleavage where the apex and base of the endocarp meet. Holotype, USNM 354506. PC, ×4.

16. Same, viewed laterally, showing central plug. ×4.


1

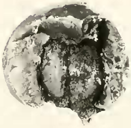

2


3


4

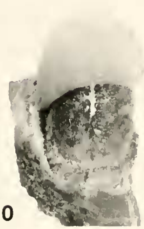

5


6


7


8


9


10

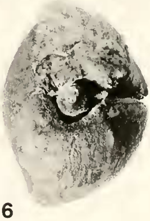

11


12


13


14


15


16


1


2


3

4


5


6


7


8


9


10


11


12

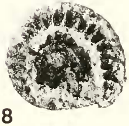

13


14

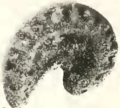

15


16


17


18


19


20

EXPLANATION OF PLATE 30

Figure — Page

1–5. *Tinomiscoidea occidentalis* sp. nov. Holotype, USNM 422382. PC, ×4. 71
- 1. Locule cast in lateral view, showing thin profile.
- 2, 3. Stereo-pair, dorsal view showing pointed apex and base and median keel.
- 4, 5. Stereo-pair, ventral view with shallow condylar cavity, prominent median keel, and subapical placental scar (arrow).

6–10. *Atriaecarpum clarnense* sp. nov. Holotype, UF 9257. PC, ×4. 71
- 6. Locule cast in lateral view showing thin profile.
- 7, 8. Stereo-pair, dorsal view showing shallow pits and very faint median keel.
- 9, 10. Stereo-pair, ventral view with pronounced pitting and prominent median keel.

11–14. *Diploclisia auriformis* (Hollick) comb. nov. ×5. 73
- 11. Edge view of a locule cast limb protruding from matrix, showing characteristic sculpture, surrounded by the dark outline of the endocarp mold. Note the three-angled apical rim of the endocarp. UF 6485.
- 12, 13. Stereo-pair of horseshoe-shaped locule cast and carbonaceous endocarp remains in matrix, showing fluted rim and central foramen. UF 6484.
- 14. Locule cast with one limb broken, showing placental "knob" and evenly spaced fluting. UF 6486.

15–20. *Palaeosinomenium venablesii* Chandler. PC, ×6.5. 74
- 15. Mold, face view, in siltstone showing endocarp ornamentation. UF 9545.
- 16. Edge view of an endocarp cast. USNM 354561.
- 17, 18. Stereo-pair of same showing numerous flutings along the rim. USNM 354561.
- 19. Locule cast showing smoother contours than do the endocarps (figs. 17, 18) and pronounced sinus between the uneven limbs. USNM 354562.
- 20. Larger locule cast with more asymmetrical limbs. UF 6487.

EXPLANATION OF PLATE 31

Figure — Page

1–5. *Curvitinospora formanii* gen. et sp. nov. Holotype, USNM 326714. PC, ×8. 71

- 1. Dorsal view of locule cast, showing prominent median keel, rounded base and pointed apex.
- 2, 3. Stereo-pair, ventral view, showing longitudinal depressions on either side of the median raphe ridge.
- 4, 5. Stereo-pair, lateral view with ventral surface to the right, showing longitudinal curviture.

6–9. *Thanikaimonia geniculata* gen. et sp. nov. Holotype, USNM 355480 PC, ×6.5. 75

- 6. Face view of lateral limb, showing smooth surface, basally tapered profile, and longitudinal median keel.
- 7, 8. Stereo-pair, lateral view, showing curvature.
- 9. Basal view, showing attachment scar and unequal development of the limbs.

10–14. *Davisicarpum limacioides* sp. nov. Holotype, USNM 435054. 73

- 10, 11. Stereo-pair, permineralized endocarp, lateral view showing curved dorsal ridge with fine radially oriented striations and concave base of the endocarp partially embedded in sediment. RL, ×7.
- 12. Same, edge view with plane of bisymmetry medial, showing median dorsal keel and the convex lateral margins of the fruit, best seen on the left side. RL, ×7.
- 13. Same, sectioned transversely at right angles to the plane of symmetry, showing diamond-shaped locule at top of specimen, endocarp walls that bulge and thicken around the condyle. RL, ×10.
- 14. Same, showing detail of seed coat within locule and thin surrounding endcarp wall. RL, ×40.


1


2

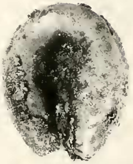

3


4


5


6

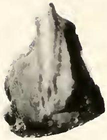

7


8


9

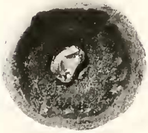

10


11


12


13

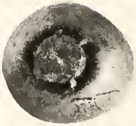

14


1


2

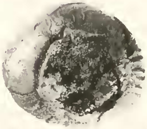

3

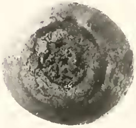

4


5


6


7


8


9


10


11


12


13

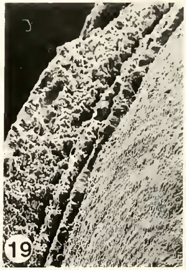

14


15


16


17


18


19

EXPLANATION OF PLATE 32

Figure Page

1–14. *Ensete oregonense* Manchester et Kress. 75

1. Apical view of permineralized seed showing round profile and cicular hilum. Holotype, UF 6621. PC, ×5.
2. Lateral view of seed with fibrous seed coat partially broken away exposing smooth endocarp cast, upper right. UF 6627. PC, ×5.
3. Lateral view of seed with portion of seed coat broken away and exposing the silica infilling of the central chamber. UF 6611. PC, ×5.
4. Internal mold of seed coat showing the prominent micropylar plug with protruding beak. UF 6623. PC, ×5.
5. Apical view of the same specimen, showing intact plug. PC, ×5.
6. Lateral view of the specimen in fig. 1 showing striate seed coat and apical truncation from which the operculum has detached. PC, ×5.
7. Basal view of the specimen in fig. 2 with chalazal mass exposed through the broken seed coat. PC, ×5.
8. Basal view of the specimen in fig. 3, showing chalazal mass and ribbing of the seed coat. PC, ×5.
9. Basal view of the specimen in fig. 4, showing position of chalaza. PC, ×5.
10. Specimen with micropylar plug removed. OMSI Pb1314. PC, ×5.
11. Median longitudinal section of the holotype in figs. 1, 6, showing silica-filled central endosperm chamber separated by a basal septum from the chalazal mass and by and apical septum with a central pore from the operculum. RL, ×5.
12. Median longitudinal section of the specimen in figs. 2, 7, showing two-layered seed coat, lower right, and intact embryo at the apex of the central chamber. RL, ×5.
13. Detail of the embryo from fig. 12. ×8.
14. Detail of the specimen in fig. 11, showing two-layered seed coat. ×8.

15. Extant *Ensete glaucum* (Roxb.) Cheesman. Seed sectioned longitudinally for comparison with figs. 11–14. Marobe District, Papua New Guinea. Kress 83-1554 (US). ×3. 76

16. *Ensete oregonense* seed cast in siltstone showing intact apical operculum, OMSI Pb1061. ×5. 75

17–19. Detail of the specimen in fig. 10, showing construction of the seed coat. 75

17. Oblique apical view of the inner mold of seed coat showing concave surface with central circular hilar scar. SEM, ×15.
18. Lateral view showing longitudinally striate seed coat partially broken away from the endosperm cast, revealing smooth inner surface. SEM, ×50.
19. The same, apical view, showing relative thickness and stratification of seed coat. SEM, ×75.

EXPLANATION OF PLATE 33

Figure Page

1–3. *Sabal bracknellense* (Chandler) Mai, seed casts. 76

1. Lateral view of seed showing raphe groove and protrusion of embryo. UF 8487. PC, ×6.

2, 3. Same, stereo-pair, ventral face showing circular depression with central raised chalazal mound and raphe groove. PC, ×6.

4–8. *Sabal jenkinsii* (Chandler) comb. nov., seed casts. 77

4. Ventral view, showing the circular depression, central chalazal mound, and raphe groove. UF 9751. PC, ×5.

5. Lateral view showing groove and chalazal mound. OMSI Pb1812. PC, ×5.

6. Same, ventral view showing chalazal mound within circular depression. PC, ×5.

7. Specimen showing elliptical pad of tissue surrounding the chalazal mound. PC, ×5. UF 9752.

8. Transverse section showing bi-layered seed coat. UF 9754. RL, ×65.

9–14. *Macginicarpa glabra* Manchester. 77

9. Infructescence broken transversely showing radiating florets of mature fruits and the receptacular impressions indicating five free carpels per floret. Holotype, UF 5153. RL, ×3.

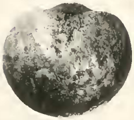
10. Tangential section of silicified infructescence, showing five-fruited florets. UF 5159. Etched, RL, ×5.

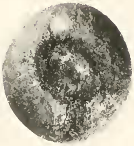
11. Transverse section of an infructescence, showing florets, with fruits and perianth in longitudinal section. UF 5158. RL, ×4.5.

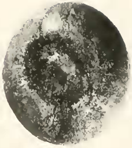
12. Same specimen as Figure 10, detail of a fruitlet in transverse section showing layers of pericarp and surrounding the locule with a single seed. TL, ×50.

13. *Platananthus synandrus* Manchester, staminate inflorescences possibly from the same plant as *M. glabra.* Inflorescence sectioned medially showing florets with stamens enveloped by well-developed perianth. UF 5151. ×7. 78

14. *Platanus hirticarpa* sp. nov., medial section of infructescence, showing numerous radiating florets. Holotype, UF 5160. ×7. . . . 78


1

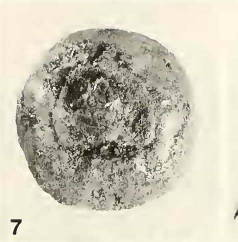

2


3


4

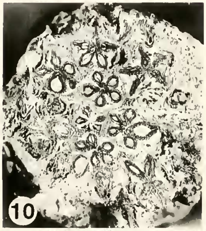

5


6


7


8


9


10


11


12


13


14


1


2

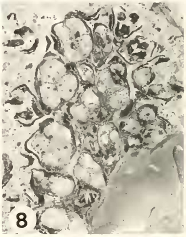

3


4

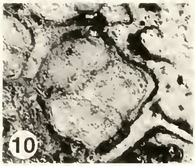

5

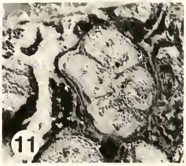

6


7


8


9


10


11


12


13


14


15

EXPLANATION OF PLATE 34

Figure		Page
1–4.	*Platanus hirticarpa* sp. nov. Continued from Pl. 33, fig. 14. Holotype, UF 5160.	78
	1. Oblique peripheral section, showing perianth, hairs and individual achenes. RL, ×20.	
	2. Longitudianal section through two achenes with obtriangular outlines with the surrounding perianth of a single floret. RL, ×20.	
	3. Longitudinal section of an achene with typical persistent style. RL, ×20.	
	4. Longitudianl section through the dispersal hairs of an achene. RL, ×50.	
5–15.	*Tanyoplatanus cranei* gen. et sp. nov.	78
	5. Longitudinally broken infructescence in matrix, showing achenes attached to central axis. UF 5671. ×4.	
	6. Same, transverse section showing circular central axis with radiating achenes. RL, ×8.	
	7. Same, median longitudinal section through the axis with rows of achenes on either side. Note protruding perianth segments. RL, ×8.	
	8. Tangential section of the infructescence showing three- and four-carpeled florets. RL, ×8.	
	9. Median longitudinal section showing clusters of at least two carpels. RL, ×8.	
	10. Detail from fig. 8, showing three closely adhering carpels surrounded by perianth segments. RL, ×20.	
	11. Same, with four closely adhering achenes. RL, ×20.	
	12. Longitudinally fractured infructescence larger than that in fig. 5. Holotype, USNM 424876. ×3.	
	13. Same, tangential section of infructescence showing three- and four-carpeled florets. ×16.	
	14. Same, transverse section of fruits, enlarged to show dispersal hairs distributed between the achenes. ×50.	
	15. Same, oblique-longitudinal section of achenes including one with elliptical seed preserved in white silica. ×20.	

EXPLANATION OF PLATE 35

Figure Page

1–10. *Prunus olsonii* sp. nov. 79

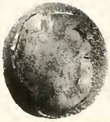
  1. Locule cast, lateral view, showing pyriform shape. UF 6461. PC, ×5.
  2, 3. Stereo-pair, base, showing thin layer partially broken away revealing circular chalaza. UF 6460. PC, ×5.7.
  4. Same, lateral view. PC, ×5.8.
  5. Same, apical view, showing apical keel. PC, ×5.6.
  6, 7. Stereo-pair, specimen with adhering testa and sedimentary matrix, showing circular chalaza and raphe groove. Holotype, UF 9262. PC, ×5.
  8. Same specimen, transverse section showing elliptical outline and thickness of the endocarp wall. PC, ×6.
  9. Same, thin section showing locule lining surrounded by sclereids. RL, ×75.
  10. Same, detail of endocarp wall showing sclereids with scattered rhomboidal crystals (arrows). TL, ×300.

11–15. *Prunus weinsteinii* sp. nov. Holotype, UF 6800. 80

  11. Lateral view of permineralized endocarp showing keel in plane of symmetry, ovate outline and gently verrucate surface. PC, ×4.
  12. Face view showing ovate-elliptical outline, and thicker funicular margin, right side. PC, ×4.
  13. Transverse section showing thick wall with plane of dehiscence near bottom of figure in plane of bisymmetry. RL ×6.
  14. Same, enlarged, showing partially detached locule lining, left side of figure. RL ×25.
  15. Detail of sclereids composing the endocarp. TL, ×100.

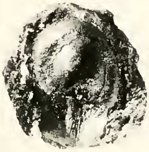

1

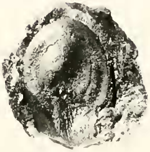

2


3


4

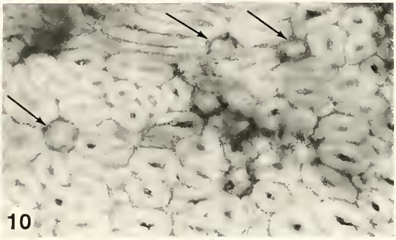

5


6

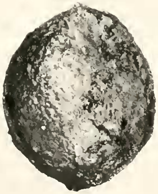

7


8


9

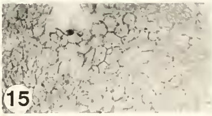

10


11


12


13


14


15


1

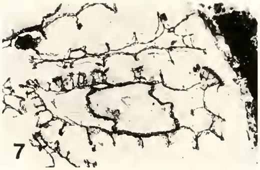

2

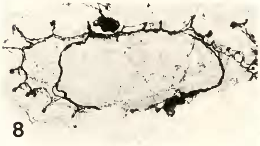

3


4


5

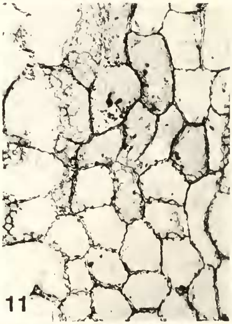

6


7


8


9


10


11


12


13

EXPLANATION OF PLATE 36

Figure Page

1–11. *Emmenopterys dilcheri* sp. nov. 80

1. Infructescence with elongate, pedicellate capsules. Scar at arrow indicates the position of a detached fruit, suggesting opposite arrangement of fruits. OMSI Pb1307b. ×1.
2. Infructescence with portions of three attached permineralized capsules. The one on the right is nearly complete. Note absence of perianth scars at the junction of the pedicels with the fruits, indicating inferior ovaries. Holotype, OMSI Pb1197b. ×2.
3. Detail of capsule from the counterpart of specimen in fig. 2, showing longitudinal median septum. Holotype, OMSI Pb1197a. ×2.5.
4. Transverse section of a capsule from the specimen in fig. 2, showing two carpels with axile placentation, and relatively thin pericarp. RL, ×8.
5. Transverse thin section of the same, showing a T-shaped placenta, surrounded by numerous radially arranged seeds. TL, ×12.

6–11. Acetate peels of permineralized fruit. UF 9333.

6. Transverse section showing well preserved seeds surrounding collapsed placenta, and a portion of remaining pericarp. TL, ×12.

7, 8. Detail of individual seeds in transverse section, each with a central body surrounded by a thin dark layer, which is in turn loosely enveloped by the seed coat formed of a reticulum of cells with projecting anticlinal walls, and thin, mostly collapsed, outer periclinal walls. TL, ×50.

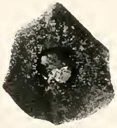
9. Longitudinal section through a seed. TL, ×30.
10. Longitudinal, peridermal section of a seed, showing reticulate seed coat. ×25.
11. Detail of seed coat showing reticulate thickening of cells composing the seed coat. ×65.

12, 13. Extant *Emmenopterys henryi* Oliver. Southwest China. G. Forrest 26041 (US 1377648). 81

12. Isolated seed showing dark elliptical central body surrounded by thin reticulate patterned wing. ×10.
13. Detail of seed coat showing reticulate thickening of cells composing the seed coat, cf. figs. 10, 11. × 25.

EXPLANATION OF PLATE 37

Figure		Page
1–5.	*Meliosma beusekomii* sp. nov. PC, ×7.	82
	1. Endocarp, ventral view, showing angular outline, circular funicular plug, rounded basal flank. UF 6702.	
	2. Same, lateral view, showing curvature of dorsal surface.	
	3. Locule cast, ventral view, showing funicular opening and median longitudinal keel. Note punctate surface. Holotype, UF 6673.	
	4. Same, basal view, showing punctate surface and median keel.	
	5. Same, lateral view showing height (vertical dimension) similar to length (horizontal dimension).	
6–9.	*Meliosma bonesii* sp. nov. PC, ×5.	82
	6. Endocarp, ventral view, showing prominent funicular cavity, rounded-triangular outline and relatively flat basal flank. UF 6715.	
	7. Endocarp, ventral view, with funicular plug and relatively flat basal flank. Holotype, UF 6714.	
	8. Same, dorsal view, showing median longitudinal keel and rounded outline.	
	9. Same, lateral view, showing rounded dorsal surface and truncate ventral side.	
10–12.	*Meliosma elongicarpa* sp. nov. Holotype, UCMP 10701. ×5.	82
	10. Ventral view showing rounded sides, median keel and circular funicular plug.	
	11. Same, basal view (cf. fig. 4), showing funicle, median keel and height much greater than width.	
	12. Same, lateral view (cf. fig. 2).	
13–15.	*Meliosma* cf. *jenkinsii* Reid et Chandler. PC, ×4.	84
	13. Ventral view of a locule cast with some endocarp adhering (upper right), showing large overall size and large funicular plug. UF 6706.	
	14. Same, dorsal view, showing smooth locule surface and median longitudinal keel.	
	15. Locule cast, ventral view, with some of the endocarp preserved in the funicular area. UF 6707.	
16–19.	*Meliosma leptocarpa* sp. nov. Holotype, UF 6725. PC, ×6.	83
	16. Ventral view showing circular funicular plug, median keel and narrow width.	
	17. apical view showing height much greater than width.	
	18–19. Stereo-pair, lateral view.	

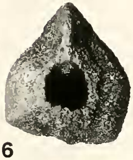

1

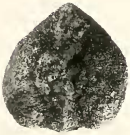

2


3


4

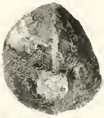

5


6


7

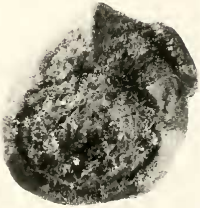

8


9


10


11


12


13


14


15


16


17


18


19

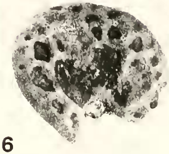

1

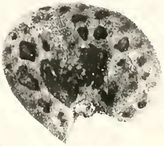

2


3


4

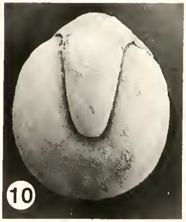

5


6


7


8

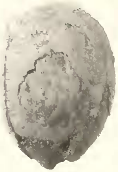

9


10


11


12


13


14


15


16

EXPLANATION OF PLATE 38

Figure		Page
1–4.	*Meliosma* endocarps in longitudinal section in the plane of bisymmetry. RL, ×5.5.	82
1.	*Meliosma beusekomii* sp. nov. UF 6683.	82
2.	*Meliosma bonesii* sp. nov. UF 6712.	82
3.	*Meliosma* cf. *jenkinsii* Reid et Chandler. UF 9851.	84
4.	*Meliosma leptocarpa* sp. nov., longitudinal section. UF 6739.	83
5–8.	*Sabia prefoetida* (Becker) comb. nov. PC, ×8.	84
5.	Endocarp cast, lateral view, showing cratered surface and ventral notch. UF 6729.	
6–7.	Stero-pair, lateral view. Note funicle scar within the ventral notch. UF 5245.	
8.	Same, viewed from base, showing circular funicle scar, endocarp thickness and median keel in the plane of symmetry.	
9, 10.	*Palaeoallophylus globosa* sp. nov. SEM, ×8.	86
9.	Chalcedony embryo cast, lateral view, showing globose outline, convoluted cotyledons and curved radicle. UF 6589.	
10.	Face view of cast, showing wide elliptical, nearly circular, outline, and the U-shaped tip of the radicle. Holotype, UF 6587.	
11–16.	*Palaeoallophylus gordonii* sp. nov.	86
11.	Chalcedony embryo cast showing convoluted cotyledons and elongate radicle. USNM 424668. SEM, ×8.	
12.	Embryo cast with portion of seed coat adhering, upper right. UF 6596. SEM, ×8.	
13, 14.	Stereo-pair, chalcedony seed cast with portion of testa flaked away showing convolutions of embryo cast and basal protrusion of the hilum. Holotype, USNM 424669. PC, ×8.	
15, 16.	Stereo-pair of same, basal view. Note hilar projection near the center. PC, ×8.	

EXPLANATION OF PLATE 39

Figure Page

1–6. *Deviacer wolfei,* gen. et sp. nov. 85
- 1. Samara showing broad lateral wing with arching dichotomous venation and elliptical endocarp with straight margin of abscission aligned with the stipe. Holotype, OMSI Pb1133. ×2.2.
- 2. Similar fruit. OMSI Pb567. ×2.2.
- 3. Larger specimen, showing style (s) arising from the elliptical endocarp. OMSI Pb638. ×2.2.
- 4. Specimen showing reticulate venation over the endocarp. OMSI Pb1786. ×2.2.
- 5. Specimen with narrower wing. OMSI Pb802. ×2.5.
- 6. Well preserved smaller specimen with recurved style from Clarno White Cliffs locality. UF 9859. ×4.

7–16. *Bumelia*? *globosa* sp. nov., internal molds of the seed coat. 86
- 7. Lateral view, showing smooth, rounded base and sides and the oblique apical truncation. USNM 424663. PC, ×6.5.
- 8, 9. Same, stereo-pair, apical view, showing circular hilar truncation, and position of micropyle (m). PC, ×6.5.
- 10. Translucent seed cast, ventral view, showing median longitudinal course of the raphe. USNM 424662. RL, ×6.5.
- 11. Same, apical view, showing emergence of raphe at center of hilar truncation. RL, ×6.5.
- 12. Lateral view showing smooth rounded sides and oblique truncation. Holotype, USNM 424644. PC, ×6.
- 13, 14. Same, stereo-pair, apical view, showing raphe that passes from ventral (lower) surface to the apical truncation and adhering vascular reticulum. PC, ×6.
- 15, 16. Same, ventral view, showing median longitudinal course of raphe. PC, ×6.5.

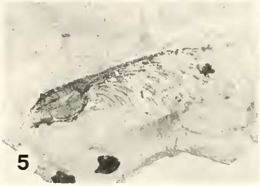
17–21. *Bumelia*? *subangularis* sp. nov., seed casts. 87
- 17. Lateral view of seed cast showing smooth surface, rounded base and oblique apical truncation. USNM 424681. PC, ×6.
- 18. Same, apical view, showing rounded-triangular outline, rounded rim of the hilar truncation, and central hilum.
- 19. Holotype, lateral view. UF 8743. PC, ×6.
- 20. Same, ventral view.
- 21. Same, apical view, showing obovate truncation with central hilum from which veins radiate, with a fragment broken away near the micropyle.

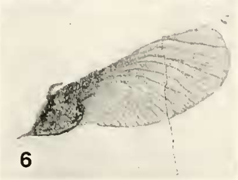

1

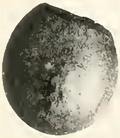

2

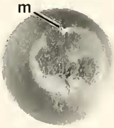
3


4


5


6

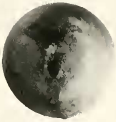

7



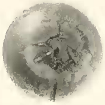
8

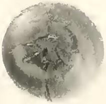

9

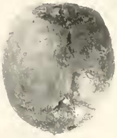

10


11


12


13

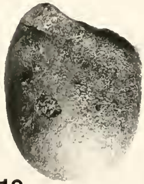

14


15


16

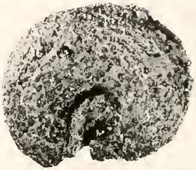

17

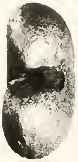

18

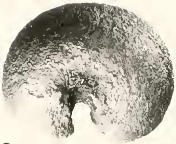

19


20


21


1


2

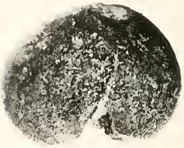

3


4


5


6

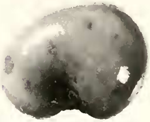

7

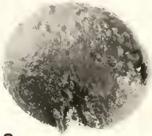

8

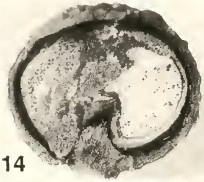

9

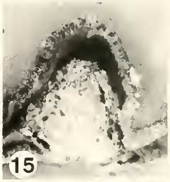

10


11

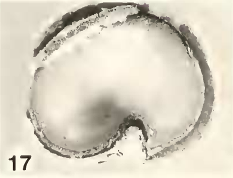

12


13


14


15


16


17


18

EXPLANATION OF PLATE 40

Figure Page

1–11. *Schisandra oregonensis* sp. nov. 87

1. Complete seed cast showing veruccate surface and hilar sinus with bulging lip. UF 6577. ×8.
2. Seed cast (internal mold of tegmen), ventral view. USNM 424654. ×6.5.
3. Same, lateral view, showing indented hilar region. PC, ×6.5.
4. Seed with tapering micropylar limb and deep hilar region. Holotype, USNM 424655. PC, ×7.5.
5. Same, tilted to show path of raphe along dorsal surface. SEM, ×10.
6. Same, ventral view. SEM, ×8.
7. Same, sectioned dorsiventrally, showing layer of columnar cells making up the seed coat, and dorsal position of the raphe (arrow). RL, ×15.
8. Seed cast (internal mold of tegmen). UF 6581. RL, ×6.5.
9. Same specimen as 2, 3, sectioned longitudinally. RL, ×10.
10. Same specimen as in fig. 8, sectioned longitudinally. RL, ×8.
11. Same, showing uniseriate columnar layer of the tegmen. RL, ×20.

12–18. Extant seeds. 88

12. *Schisandra chinensis* Baill. Seed with smooth surface. Shinano Province, Japan, Sept., 1960. Miyoshi Furuse (A). ×8.
13. *Schisandra viridis* A.C. Smith. Seed with rought surface and hilar sinus with bulging lip. Cf. fig. 1. Chekiang, China. Ren-Chang Ching 5132 (A). ×8.
14. Same, sectioned longitudinally, ×11.
15. *Kadsura japonica* Dunal. Longitudinally sectioned seed. Ohobu, Kobe, Japan. H. Muroi 6569 (A). RL, ×30.
16. *Schisandra chinensis*. Same as fig. 12, sectioned longitudinally. RL, ×10.
17. *Kadsura japonica*, sectioned longitudinally, same as fig. 15. RL, ×10.
18. *Schisandra viridis*, sectioned longitudinally. Note columnar inner layer of seedcoat, and proliferation of isodiametric cells of the outer seed coat filling the hilar sinus. Same as figs. 13, 14. ×20.

Explanation of Plate 41

Figure — Page

1–9. *Tapiscia occidentalis* Manchester. — 88

1. Chalcedony fruit cast, ventral view, with features of the seed expressed through the thin wrinkled pericarp, including the central circular chalaza, raphe, and pedicel scar (top of figure). UF 5201. PC, ×7.5.
2. Same, dorsal view, showing rugulate ornamentation. RL, ×7.5.
3. Ventral view of fruit cast with verrucate surface layer partially broken away revealing internal mold of seed coat with prominent circular chalaza at the center and pointed micropyle at the apex. Holotype, UF 5200. PC, ×7.5.
4. Permineralized fruit in matrix, ventral view. UF 9283. RL, ×7.5.
5. Internal mold of seed with successive layers of seed coat and pericarp adhering. UF 9692. SEM, ×10.
6. Same, cellular detail on surface of internal seed coat mold. SEM, ×150.
7. Median lateral section of the specimen from fig. 4, showing thickness of fruit wall and seed coat layers, c-shaped endosperm cavity conforming around the chalazal complex (right side). UF 9283. RL, ×10.
8. Transverse section, showing endosperm within the seed. UF 9284. RL, ×10.
9. Same, transverse section enlarged to show anticlinally oriented cells of seed coat. RL, ×50.

10–17. *Symplocos nooteboomii* sp. nov. — 89

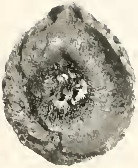
10. Chalcedony endocarp cast, lateral view, showing truncate apex, rounded base and meridional grooves. Holotype, USNM 354596. PC, ×3.
11. Same, basal view, showing central attachment scar surrounded by radiating meridional grooves. PC, ×3.

12, 13. Stereo-pair of same, apical view, showing four apertures on the apical truncation. PC, ×3.

14. Another specimen, showing the apical truncation and meridional ribs, broken below. USNM 354603. PC, ×3.8.
15. Same, apical view, showing at least two apertures within the truncation. PC, ×3.9.
16. Chalcedony endocarp cast, lateral view. USNM 354592. PC, ×5.7.
17. Same, basal view. PC, ×5.9.

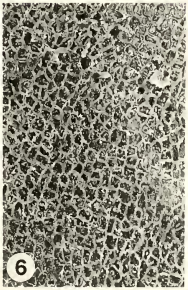

1


2


3

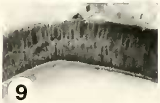

4


5

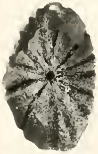

6


7


8


9

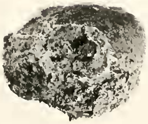

10


11


12


13


14


15


16


17


1


2


3


4


5


6


7


8


9


10

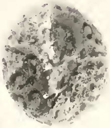

11

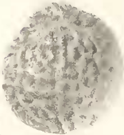

12


13


14


15

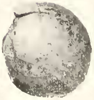

16


17


18


19


20


21


22


23


24


25

EXPLANATION OF PLATE 42

Figure Page

1–5. *Cleyera grotei* sp. nov. 89

1. Seed, lateral view, showing reticulate seed coat. Holotype, UF 6501. SEM, ×15.
2. Same, basal view showing thickness of seed. SEM, ×16.
3. Internal cast of seed coat, lateral view, showing embryo curving around the condyle. UF 9449. SEM, ×15.
4. Internal cast of seed coat, showing condyle in center and possibly the micropylar limb on the left, UF 9450. SEM, ×19.
5. Detail from holotype, fig. 1, showing thick anticlinal walls of cells forming the seed coat. SEM, ×50.

6–15. *Aphananthe maii* sp. nov. 90

6. Silicified endocarp, apical view, showing rounded contour, median ridge and elliptical obliquely oriented funicular pore. The median ridge is deflected laterally at the funicular opening. Holotype, USNM 355693. PC, ×5.
7. Same, lateral view, showing wide-elliptical outline and verrucate surface. PC, ×5.
8. Endocarp, apical view, with obliquely oriented funicular pore. Lower portion of endocarp wall broken away exposing smooth, rounded locule cast. USNM 424629. PC, ×5.
9. Chacedony locule cast, showing smooth surface and well-marked longitudinal keels that intersect at the funicular pore. UF 6518. PC, ×5.
10. Same, lateral view showing relatively narrow elliptical outline. PC, ×5.
11. Locule cast, apical view, surrounded by remains of the endocarp wall. USNM 422384. SEM, ×7.5.
12. Some of the endocarp wall removed from the specimen in fig. 11, showing layer lining the locule. SEM, ×10.
13. Longitudinal section of a well preserved endocarp fragment showing dark wall of endocarp surrounding coiled embryo. UF 9328. RL, ×8.
14. Section of wall from the holotype, figs. 6, 7, showing outer layer of prismatic cells including crystaliferous inflated cells. RL, ×20.
15. Detail of wall from fig. 13 showing large columnar cells. TL, ×60.

16–25. *Celtis burnhamae* sp.nov. 91

16. Endocarp, apical view, showing nearly circular outline, reticulate surface pattern and four longitudinal ribs. Holotype, UF 9600. PC, ×6.
17. Same, lateral view, showing median longitudinal rib, reticulate smaller ribs. PC, ×6.
18. Same, rotated 90°, showing primary longitudinal rib and acute apex. PC, ×6.
19. Same, basal view showing intersection of four median ribs. PC, ×6.
20. Locule cast showing smooth surface, circular chalaza, and radicle at top of figure. USNM 355429. PC, ×6.
21. Same, lateral view, showing curved radicle. PC, ×6.
22. Longitudinal section of permineralized specimen, showing single locule filled by the embryo which has a curved, protruding radicle. Note thickness of endocarp and subapical position of funicular plug. UF 9581. ×10.
23. Transverse section of fruit, showing large, nearly circular locule surrounded by successive layers of the pericarp. UF 9581. ×10.
24. Detail of same, with locule to the left showing succession of pericarp layers, the most prominent of which is the uniseriate layer of square crystaliferous cells. RL, ×15.
25. Detail of internal surface with digitate cells. Seen by focusing down through the outer translucent part of the pericarp. UF 8626. RL and TL, ×35.

EXPLANATION OF PLATE 43

Figure — Page

1–5. *Celtis* sp. 92

- 1. Silicified endocarp, face view, showing median longitudinal keel, apical attachment scar and veruccate surface ornamentation. UF 8658. SEM, ×6.
- 2. Same, lateral view showing apical notch, rounded outline and typical surface ornamentation. PC, ×6.
- 3. Lateral view of an endocarp with part of the wall fractured away, revealing locule cast with prominent curved radicle. UF 8641. SEM, ×6.
- 4. Transverse section of an endocarp. Horizontal line is the separation between radicle and the rest of the embryo. UF 8651. RL, ×10.
- 5. Same, enlarged to show wall anatomy. RL, ×30.

6–15. *Trema nucilecta* sp. nov. 92

- 6. Silicified endocarp, dorsal view, showing median longitudinal keel, ovate outline, and relatively smooth surface. Holotype, UF 9781. SEM, ×15.
- 7. Same, lateral view. RL, ×10.
- 8. Same, sectioned longitudinally, showing coiled embryo of the seed, with pronounced radicle. RL, ×10.
- 9. Transverse section, showing thickness of wall and horizontal line separating the radicle from the rest of the embryo. UF 9776. RL, ×10.
- 10. Same, enlarged, showing columnar cells of endocarp wall. RL, ×50.
- 11–13. Isolated locule casts.
  - 11. Dorsal view showing median keel. UF 6792. PC, ×10.
  - 12. Ventral view. UF 6793. PC, ×10.
  - 13. Lateral view. UF 6792. PC, ×10.
- 14. Longitudinal section, showing complexity of the apical region. UF 9585. ×10.
- 15. Same, showing columnar cells of the endocarp wall. ×18.

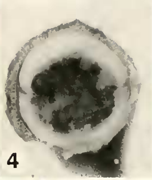
16–18. *Cedrelospermum lineatum* (Lesquereux) Manchester. 92

- 16. Typical samara showing large wing with veins converging toward the stigmatic area, and small wing forming a crest along part of the endocarp. OMSI Pb565. ×4.5.
- 17. Smaller samara. OMSI Pb1502. ×5.
- 18. Fruit showing the small wing extending parallel to the long axis of the endocarp. UF 9285. ×6.


1


2


3


4


5


6

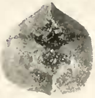

7


8


9


10


11

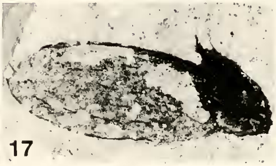

12


13


14


15


16


17

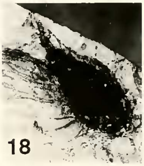

18

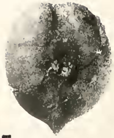
PLATE 44


1


2


3


4

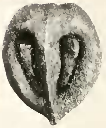

5


6

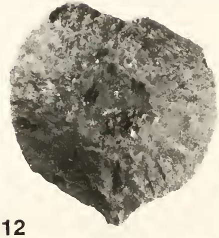

7


8


9


10


11


12


13


14


15


16


17


18


19


20


21


22

EXPLANATION OF PLATE 44

Figure Page

1–5. *Vitis tiffneyi* sp. nov. 96

1. Chalcedony seed cast, ventral view, showing short parallel infolds, and prominent median groove along the raphe ridge. Holotype, UF 6534. PC, ×7.8.
2. Same, dorsal view, showing spatulate chalaza and chalaza-apex groove. PC, ×8.
3. Dorsal view of a seed cast with much of the seed coat flaked away revealing internal mold of the seed cavity with circular chalazal mark. UF 6533. PC, ×8.
4. Chalcedony internal mold of seed coat, ventral view, showing sharply pointed base and parallel infolds. UF 6535. PC, ×8.
5. Same, dorsal view showing chalaza-apex groove. PC, ×8.

6–10. *Ampelopsis rooseae* sp. nov. 94

6. Chalcedony seed cast, ventral view, showing short divergent infolds, and median groove along the raphe ridge. UF 6537. PC, ×8.
7. Same, dorsal view, with portion of seed coat flaked away, revealing smooth internal mold of the seed cavity. Note chalaza-apex ridge (contrast with chalaza-apex groove, figs. 2, 3, 5). PC, ×8.
8. A broader seed cast with widely divergent infolds. Holotype, UF 6536. PC, ×8.
9. Same, dorsal view, showing spatulate chalaza, chalaza-apex ridge and chalaza-base groove. PC, ×8.
10. Chalcedony internal mold of seed coat, ventral view, showing pointed base, sharp raphe ridge, and prominent, divergent infolds. UF 6538. PC, ×8.

11–15. *Ampelocissus scottii* sp. nov. 94

11. Seed cast, ventral view, showing cordate outline and short, divergent ventral infolds. Holotype, USNM 424665. PC, ×8.
12. Same, dorsal view. PC, ×8.
13. Internal cast of seed cavity, ventral view, showing prominent short ventral infolds and sharply pointed base. UF 6542. PC, ×8.
14. Same, lateral view, showing split along dorsiventral plane. PC, ×8.
15. Same, dorsal view, showing elliptical chalaza and shallow chalaza-apex groove. PC, ×8.

16–18. *Ampelocissus auriforma* sp. nov. 93

16. Chalcedony internal mold of seed coat, ventral view, showing width and depth of infolds and cordate outline. UF 6543. PC, ×6.
17. Same, dorsal view, showing elliptical chalaza and chalaza-apex and basal groove. PC, ×6.
18. Chalcedony internal mold of seed coat cavity with corresponding external mold of the same seed showing ventral infolds as a pair of mounds in the siltstone matrix. Holotype, UF 6572. ×3.75.

19. *Vitis tiffneyi* sp. nov. Transverse section showing deep ventral infolds and relatively narrow seed coat. UF 9573. RL, ×12.5. 96
20. Same, enlarged greater to show columnar cells of seed coat. RL, ×30.
21. *Ampelopsis rooseae* sp. nov. Transverse section showing relatively thick seed coat. UF 9575. RL, ×12.5. 94
22. *Ampelocissus auriforma* sp. nov. Transverse section showing broad ventral infolds and thick seed coat. UF 6571. RL, ×6. 93

EXPLANATION OF PLATE 45

Figure Page

1–5. *Parthenocissus clarnensis* sp. nov. 95

1. Chalcedony seed cast, ventral view, showing long divergent infolds, relatively flat ventral faces meeting at the raphe ridge. Some of the seed coat is broken away apically, exposing internal cast of seed coat. Holotype, UF 6539. PC, ×8.
2. Same, dorsal view, showing smooth rounded surface and oval-spatulate chalaza. PC, ×8.
3. Another specimen with long divergent infolds. UF 6540. PC, ×8.
4. Same, dorsal view, showing spatulate chalaza. Lacking a groove between chalaza and base. PC, ×8.
5. Transverse section. UF 9583. RL, ×12.5.

6, 7. *Parthenocissus angustisulcata* Scott. USNM 434986. PC, ×6. 95

6. Ventral view, internal mold of seed coat, showing cordate outine with cleft at apex and long divergent infolds.
7. Dorsal view, showing circular chalaza and prominent chalaza-base and chalaza-apex grooves.

8–13. *Vitis magnisperma* Chandler. 95

8. Chalcedony internal mold of seed coat, ventral view, showing rounded apex and long divergent infolds. USNM 355098. PC, ×6.
9. Same, dorsal view, showing circular chalaza, radiating shallow grooves and more pronounced chalaza-apex groove. PC, ×6.
10. Largest specimen, showing long ventral infolds. USNM 355127. PC, ×5.
11. Same, dorsal view showing circular chalaza and well-developed chalaza-apex groove. PC, ×5.
12. Another specimen, showing flattened ventral face and fine radiations. USNM 434985. PC, ×5.
13. Same, dorsal view, showing obcordate chalaza with pronounced chalaza-apex groove and shallow radiating grooves. PC, ×5.

14–17. *Anonymocarpa ovoidea* gen. et sp. nov. Holotype, USNM 355614. 97

14. Lateral view, showing elliptical outline, with a portion of the pericarp broken away revealing striated inner layer. RL, ×1.5.
15. Transverse section, showing single locule surrounded by thin endocarp and exocarp. RL, ×1.5.
16. Same, showing detail of seed tissue, and endocarp, including a thin dark layer representing the locule lining. RL, ×12.5.
17. Same, more greatly magnified, showing anticlinally oriented columnar cells of the locule lining, surrounded by a thick layer of poorly preserved schlerenchyma. RL, ×50.


1

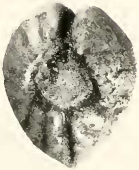

2


3


4


5


6


7


8


9


10


11


12


13


14


15


16

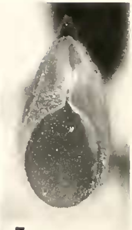

17


1


2


3


4

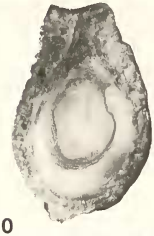

5


6


7


8


9


10


11


12


13


14


15


16


17

EXPLANATION OF PLATE 46

Figure Page

1–5. *Axinosperma agnostum* gen. et sp. nov. 97

1. Oblique ventral-lateral view, showing rounded base, pore near the apex, and apical crest. Holotype, UF 6290. SEM, ×20.
2. Ventral view, showing narrow width, median apical crest and pore. USNM 424712. SEM, ×20.
3. Lateral view of a specimen that has broken apically, showing protruding inner cast. UF 9799. SEM, ×20.
4. Same, magnified to show thickness of wall and smooth surface of inner cast. SEM, ×42.
5. Seed sectioned transversely, showing elliptical outline of inner chamber and longitudinal slit leading to the ventral pore. UF 9800. TL, ×30.

6–10. *Ascosphaera eocenis* gen. et sp. nov. 97

6. Fruit showing pyriform shape and scabrate surface. UF 6320. SEM, ×10.
7. Fruit with part of the pericarp fractured away revealing globose locule cast. Holotype, UF 6318. SEM, ×10.
8. Locule cast showing globose shape, circular chalazal scar at base, and slight apical swelling. UF 6343. SEM, ×20.
9. Locule cast, apical view, showing circular outline. UF 9770. SEM, ×20.
10. Longitudinal section of fruit in fig. 6, showing globose seed inside, ×10.

11–13. *Ankistrosperma spitzerae* gen. et sp. nov. 97

11. Specimen viewed laterally, showing J-outline. UF 9808. ×15.
12. Lateral view showing J-outline, neck-like constriction at top. Holotype, UF 9806. SEM, ×20.
13. Same, face view. UF 9807. SEM, ×20.

14–17. *Dentisemen parvum* gen. et sp. nov. SEM, ×16. 99

14. Ventral view, showing median longitudinal slit. Holotype, UF 9766.
15. Same, dorsal view, showing truncate base and pointed apex.
16. Ventral view, specimen with fractured apex. UF 9767.
17. Same, dorsal view showing veruccate surface.

Explanation of Plate 47

Figure Page

1–10. *Bonesia spatulata* gen. et sp. nov. 98

- 1–4. Chalcedony locule cast. Holotype, USNM 424642. PC, ×6.
  - 1. Face view, showing rounded scar at the base, gentle median ridge and protruding apex.
  - 2, 3. Stereo-pair, same specimen reverse side.
  - 4. Basal view, showing thin profile and prominent circular scar.
- 5–7. Chalcedony locule cast with adhering remains of pericarp. UF 9404.
  - 5. Dorsal view, showing pointed apex and rounded base. SEM, ×6.
  - 6. Same, tilted back slightly and enlarged to show circular chalaza at base. SEM, ×15.
  - 7. Detail of adhering pericarp. Punctate appearence is due to parenchyma-like cells, the outermost layer having flaked away. SEM, ×40.
- 8. Transverse section of a permineralized fruit with seed showing two horizontally oriented, parallel cotyledons. UF 9471. RL, ×15.
- 9. Transverse section of a locule cast with shriveled embryo inside consisting of two parallel, horizontally oriented cotyledons. USNM 424643. RL, ×15.
- 10. Transverse section of pericarp, detail from fig. 8, showing outer layer of columnar cells, inner layer of isodiametric cells. RL, ×30.

11–16. *Cuneisemen truncatum* gen. et sp. nov. 98

- 11. Ventral view, showing rounded sides, truncate apex and two ventral faces joining in a median keel. UF 9366. PC, ×8.
- 12, 13. Same, Stereo-pair, lateral view, showing convex dorsal side and relatively straight ventral side, disruption of tissue at the apical truncation. PC, ×8.
- 14. Ventral view, specimen tilted forward to show triangular truncation at the apex. Holotype, UF 6392. SEM, ×8.
- 15. Same, apical view. SEM, ×8.
- 16. Apical view of an asymmetrical specimen. UF 9364. SEM, ×10.


1

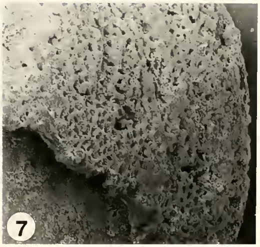

2


3


4


5


6


7

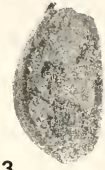

8

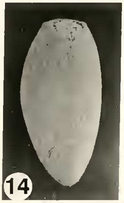

9


10


11


12

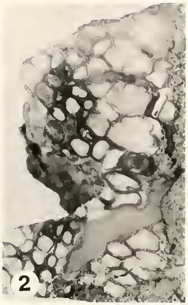

13

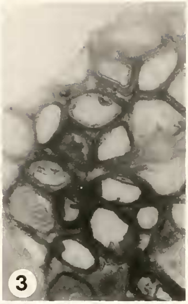

14


15


16


1


2

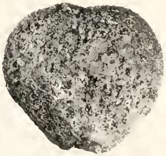

3

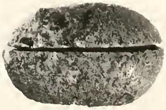

4


5


6


7

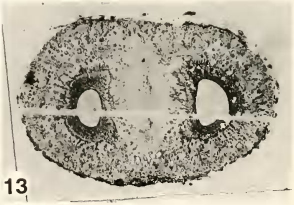

8


9


10


11


12


13

EXPLANATION OF PLATE 48

Figure Page

1–7. *Communicarpa friisae* gen. et sp. nov. 98

1. Longitudinally fractured infructescence. Holotype, USNM 355697. ×2.5.
2. Same, sectioned longitudinally, tangential to the axis, showing closely adjacent fruits in transverse section. RL, ×5.
3. Same, higher magnification, showing fruits grouped in threes. RL, ×10.
4. Another infructescence sectioned longitudinally, showing fruits in transverse section that are subangular through crowding. UF 9582. RL, ×15.
5. Same infructescence as figs. 1–3, transverse section showing fruits in longitudinal section. RL, ×6.5.
6. Same, showing detail of individual fruits including persistent style at apex and single seed per fruit. ×8.5.
7. Detail of fruits from fig. 4, showing the seed coat of a single seed within the locule and pericarp containing a middle layer of large rectangular cells. ×55.

8–13. *Durocarpus cordatus* gen. et sp. nov. Holotype, UF 6110. 99

8. Permineralized endocarp fruit, dorsal view, showing cordiform outline. PC, ×6.
9. Apical view, showing smooth, rounded contours. Horizontal line resulted from cutting longitudinally for fig. 10. PC, ×6.
10. Longitudinal section through the two locules, showing vascularization of the base and central axis, and thick fruit wall. RL, ×10.
11. Same, enlarged to show tissue surrounding the locule. Acetate peel, TL, ×30.
12. Same, enlarged to show the small, thick-walled endocarp cells lining the locules and the larger, thin-walled cells making up the bulk of mesocarp tissue. Note the placental tissue arising from the apical end of the ventral side of the locule (arrow). TL, ×50.
13. Transverse section of the same specimen, reassembled after sectioning longitudinally, showing the cross section of locules and thickness of septum. Acetate peel, TL, ×10.

EXPLANATION OF PLATE 49

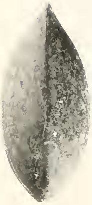
Figure — Page

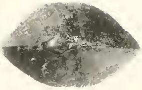
1–15. *Ferrignocarpus bivalvis* gen. et sp. nov. 99

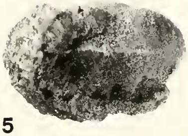
- 1. Impression of an endocarp valve in sediment, showing thickness of wall and shape of locule cast. UF 9390. ×6.
- 2–4. Locule cast showing typical smooth surface, USNM 355348. ×5.
  - 2. Face view showing elliptical outline, median longitudinal groove and slightly emarginate base.
  - 3. Lateral view showing keel in plane of symmetry with apex being slightly more acute than base.
  - 4. Apical view showing lensoidal outline.
- 5. Locule cast with adhering remains of endocarp, apical view. Holotype, USNM 424624. PC, ×6.
- 6. Permineralized endocarp in matrix, broken longitudinally showing thick endocarp wall and locule with remains of seed. UF 9391. ×5.
- 7. Isolated locule cast, face view, showing emarginate base and somewhat broken at apex. USNM 424803. ×5.
- 8, 9. Stereo pair of same specimen in fig. 5, face view showing cordiform locule cast with adhering endocarp. PC, ×6.
- 10. Transverse section of specimen in fig. 2. TL, ×5.
- 11, 12. Successive transverse sections of specimen in fig. 7, showing remains of shrunken seed in locule. RL, ×5.
- 13–15. Transverse section of specimen in figs. 5, 8 and 9.
  - 13. Section near the equator showing partial remains of endocarp, shrunken tissue within the locule and the septum. ×8.5.
  - 14. Section closer to the apex showing incomplete septum. ×8.5.
  - 15. Transverse section of the fruit wall, with locule at lower side of photo, showing two different sclerenchymatous layers. ×60.


1

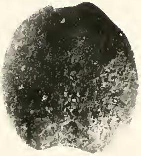

2


3


4


5

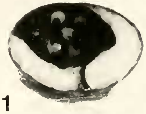

6


7


8


9

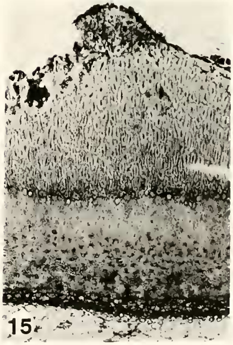

10

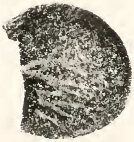

11


12


13


14

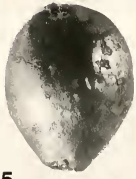

15

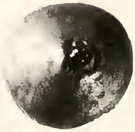

1

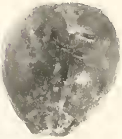

2

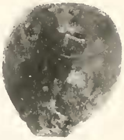

3

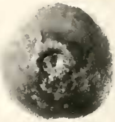

4


5


6


7


8


9


10


11


12


13


14


15


16


17


18


19

EXPLANATION OF PLATE 50

Figure Page

1–4. *Fragarites ramificans* gen. et sp. nov. 100

1. Lateral view, showing D-shape outline, and coarse, fibrous ribs. UF 9557. PC, × 10.
2. Same rotated 90°, showing hilar end and lensoidal outline. PC, × 10.
3. Another specimen, lateral view, showing rounded contour and stright hilar margin to the left. Note the network of bifurcating surface ribs. Holotype, USNM 424729. SEM, × 20.
4. Same, rotated 35°, showing the hilar area around which the surface ribs are interrupted. SEM, × 20.

5–13. *Globulicarpium levigatum* gen. et sp. nov. 101

5. Lateral view, showing smooth surface, obovate outline with pedicel projection at base. Holotype, USNM 355663. PC, × 7.
6. Same, basal view showing circular outline and central pedicel scar. PC, × 7.
7, 8. Stereo-pair of another specimen, lateral view, showing pedicel projection and rounded contours. USNM 435009. PC, × 7.
9. Same, basal view of pedicel scar. PC, × 7.
10. Larger specimen, lateral view, showing smooth surface and rounded outline. USNM 435011. PC, × 7.
11. Transverse section of the specimen in figs. 5, 6. RL, × 10.
12. Specimen in fig. 10, sectioned longitudinally, showing thickness of middle layer and globose, smooth walled locule. RL, × 8.
13. Same as fig. 11, close-up, showing the middle layer composed of isodiametric parenchyma cells and the thin inner layer surrounding the locule. RL, × 50.

14–19. *Fimbrialata wingii* gen. et sp. nov. 100

14. Seed, face view, showing elliptical seed body with encircling wing. Wing partially fractured away on left side. UF 6286. SEM, × 13.
15. Seed, lateral view, showing longitudinal wing. UF 9867. SEM, × 15.
16. Seed in face view with partially intact wing. USNM 435058. × 10.
17. Seed in face view, showing the surrounding wing which has broken in places along the left side, and showing the aril-like structure near the apex. Holotype, USNM 435057. × 10.
18. Same, median transverse section, showing wing at top of figure, broken remains of the wing at bottom of figure, and elliptical outline of endosperm within the inner seed coat. RL, × 20.
19. Same, showing two distinct layers of seed coat, and cellular makeup of the endosperm. RL, × 50.

EXPLANATION OF PLATE 51

Figure Page

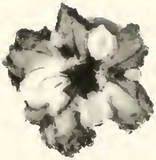
1–4. *Hexacarpellites hallii* gen. et sp. nov. Holotype, USNM 424653. 101
  1. Lateral view, showing prolate outline and longitudinal grooves. PC, ×8.
  2. Transverse section near equator, showing six radially arranged, more or less elliptical locules surrounding a prominent central axis, with each locule having one seed. RL, ×10.
  3. Transverse section near the apex, near the ends of the locules. RL, ×10.
  4. Detail of seeds within the locules, transverse section. RL, ×20.

5–8. *Joejonesia globosa* gen. et sp. nov. Holotype, UF 9260. . . . 102
  5. Basal view of endocarp, showing two valves, venose surface and nearly circular outline. ×5.
  6, 7. Stereo-pair, lateral view, broken to show thick wall, thin layer lining the smooth locule and longitudinal keel within the locule. ×5.
  8. Transverse section showing large polygonal cells making up the endocarp wall, and poorly preserved cells lining the locule. ×30.

9–16. *Lignicarpus crassimuri* gen. et sp. nov. 102
  9. Stereo-pair showing pyriform shape and coarse, longitudinally striate surface. Holotype, UF 6111. ×5.
  11, 12. Stereo-pair of same, other side, broken and revealing pyriform locule.
  13, 14. Stereo-pair of another specimen showing longitudinal ribs and striations, UF 6578. PC, ×5.
  15. Transverse section of same specimen showing thick endocarp wall and single locule. RL, ×10.
  16. Close-up of the same, showing fibers composing the endocarp wall, with interspersed clusters of smaller vascular elements. RL, ×25.

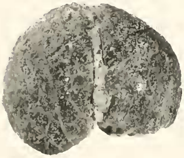
1

2



3

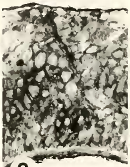
4



5

6

7



8

9

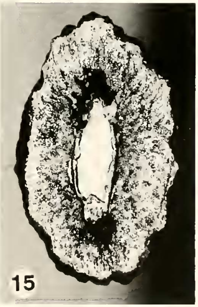
10

11

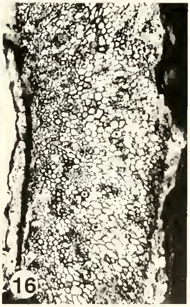
12

13

14



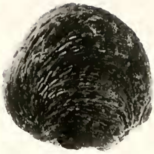
15



16


1


2

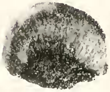

3


4


5


6


7


8


9

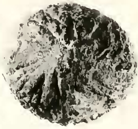

10


11


12


13


14


15


16

EXPLANATION OF PLATE 52

Figure — Page

1–12. *Lunaticarpa curvistriata* gen. et sp. nov. 103

1. Endocarp, lateral view, showing rounded margins and arched striations parallel to the outline of the dorsal margin. Holotype, USNM 435020. ×7.5.
2. Same, dorsal view showing seed thickness, bisymmetry. ×7.5.

3, 4. Stereo-pair lateral view, showing arched striations. USNM 422527. PC, ×7.5.

5. Endocarp with relatively smooth surface and faint striations. UF 6340. PC, ×7.5.
6. Endocarp, ventral view, showing circular attachment scar. USNM 435027. ×7.5.
7. Specimen with endocarp partially fractured away revealing curved locule cast. USNM 435045. ×7.5.
8. Locule cast. Lateral view, showing dorsal curvature and faint ruminations. USNM 435029. PC, ×5.
9. Same, end view, showing longitudinal keel. PC, ×5.
10. Longitudinal section of the specimen in fig. 5, showing crescent shaped seed cavity. RL, ×10.
11. Longitudinal section, showing large condyle, and seed coat. USNM 435034. TL, ×10.
12. Detail from fig. 11, showing cells of the wall adjacent to condyle, and the seed coat. TL, ×25.

13–16. *Omsicarpium striatum* gen. et sp. nov. Holotype, OMSI Pb265. 104

13. Lateral view showing ovate outline and surface striations. ×1.5.
14. Same, rotated 90 degrees. ×1.5.
15. Basal view. ×1.5.
16. Tranverse section showing single locule and thick wall. ×2.

EXPLANATION OF PLATE 53

Figure — Page

1–8. *Ligniglobus sinuosifibrae* gen. et sp. nov. 102

1. Lateral view showing more or less circular outline, persistent pedicel and fine, wavy surface striations. Holotype, UF 8483. ×1.5.
2. Same specimen, basal view, showing circular outline and radiating striations. ×1.5.
3. Same, transverse section, showing circular locule and thick wall. RL, ×1.5.
4. Smaller specimen, broken to reveal circular locule cast. USNM 354386. ×1.5.
5. Equatorial transverse section showing construction of the fruit wall. Arched line at base of figure is the locule lining. Holotype, UF 8483. RL, ×10.
6. Same, Transverse section through the mesocarp region. ×15.
7. Same, near the periphery, showing transition from mesocarp to exocarp. ×15.
8. Same, Detail of the mesocarp, showing anticlinally oriented elongate cells. ×65.

9–17. *Microphallus perplexus* gen. et sp. nov. 103

9. Ventral surface of seed showing dentral depression, radiating striations and protruding radicle. USNM 355414. PC, ×8.
10. Same, dorsal view, showing raised circular area chalaza (?) and coarse striations. PC, ×8.

11, 12. Stereo-pair of same, viewed laterally, showing raised chalazal (?) area slightly curved longitudinal axis. PC, ×8.

13. Chalcedony embryo cast, showing characteristic "screw eye" morphology. UF 5242. PC, ×8.
14. Ventral view, with smooth rounded base and shallow central depression, and protruding cast of the radicle. Holotype, UF 5243. PC, ×8.

15, 16. Same, dorsal view. PC, ×8.

17. Longitudinal thin section of a seed showing relatively thick seed coat composed mainly of large rectangular cells, surrounding a looped seed cavity with an island of tissue composed of smaller compact cells. Section is slightly oblique and therefore does not show the complete loop of the embryo. UF 6346. TL, ×15.


1


2


3


4


5


6


7


8


9


10


11


12


13

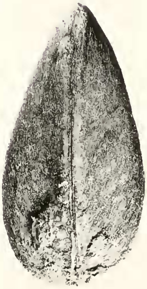

14


15


16

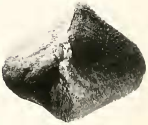

17


1

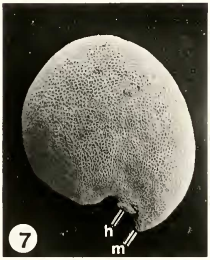

2


3

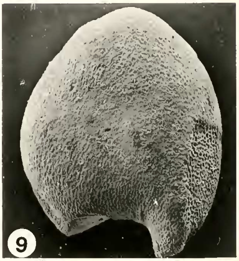

4

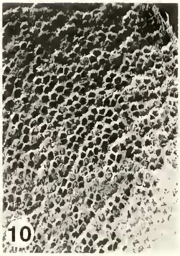

5


6


7

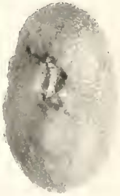

8


9


10


11


12


13

EXPLANATION OF PLATE 54

Figure Page

1–5. *Pistachioides striata* gen. et sp. nov. Holotype, USNM 422387. PC, ×3. 105
  1. Dorsal view, showing ovate shape, median longitudinal keel and faint diagonally arranged striations.
  2. Ventral view, showing continuation of the keel, rounded base and pointed apex.
  3. Lateral view rotated 90° from fig. 2, showing faint surface striations oriented diagonally from upper right to lower left.
  4. Basal view, showing rounded rhomboid outline, central attachment scar and the two valves meeting to form the keel in the plane of bisymmetry.
  5. Top view.

6–13. *Nephrosemen reticulatus* gen. et sp. nov. 104
  6. Lateral view, showing reticulate sculpture, rounded apical and lateral margins and hilar notch. USNM 355052. RL, ×15.
  7. Lateral view showing rounded outline, prominent notch with hilar scar (h) and micropylar point (m). Holotype, UF 6500. SEM, ×15.
  8. Same, ventral view, showing typical narrow thickness, details of hilum and micropyle. SEM, ×15.
  9. Lateral view of a specimen with portion of outer layer broken away revealing underlying cells. USNM 424746. SEM, ×20.
  10. Surface detail from the specimen in fig. 6. SEM, ×30.
  11. Lateral view of a seed cast with portions of surface reticulum preserved. USNM 424685. PC, ×15.
  12, 13. Same, stereo-pair, ventral view. RL, ×15.

Explanation of Plate 55

Figure — Page

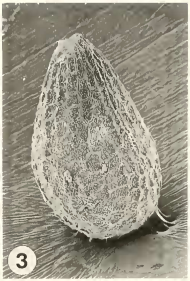
1–4. *Pasternackia pusilla* gen. et sp. nov. 104
  1. Lateral view, showing ovate outline and typical reticulate sculpture. UF 9605. SEM, ×44.
  2. Apical view, showing circular outline and meridional rows of cells. Holotype, UF 9604. SEM, ×42.
  3. Same, oblique-lateral view, showing narrower band of cells (right) that may represent course of the raphe. SEM, ×40.
  4. Another specimen, abraded apically. SEM, ×40.

5–8. *Pileosperma minutum* gen. et sp. nov. 104
  5. Internal mold of seed coat, viewed ventrally showing wide-obtuse apex, rounded base and circular "cap". Holotype, UF 6606. SEM, ×20.
  6. Another similar seed, viewed ventrally. UF 6425. SEM, ×20.
  7. Detail from fig. 5, showing a faint coarse rectagular reticulum superimposed on smaller polygonal cells. SEM, ×52.
  8. Detail of the basal end of the specimen in fig. 5, showing the circular cap. SEM, ×50.

9–11. *Pileosperma ovatum* sp. nov. 105
  9. Internal mold of seed coat, lateral view, showing uniformly angled apex, rounded base and basal cap. Holotype, USNM 424751. SEM, ×20.
  10. Another specimen, of shorter length. USNM 424755. SEM, ×20.
  11. Same, basal end, enlarged to show cells of seed coat and circular cap. SEM, ×62.


1

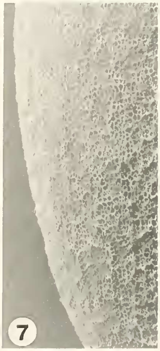

2

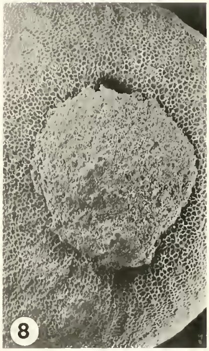

3


4


5


6


7

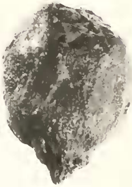

8

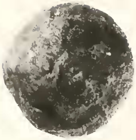

9

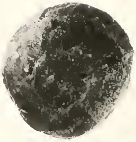

10


11

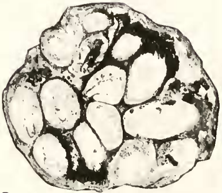

1

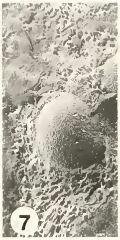

2


3

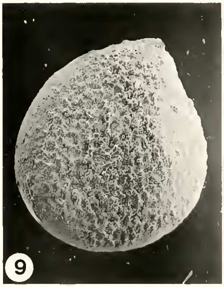

4


5


6


7


8

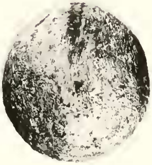

9


10

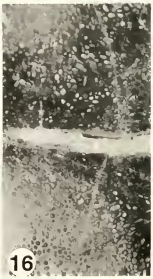

11


12


13


14


15


16

EXPLANATION OF PLATE 56

Figure Page

1–8. *Polygrana nutbedense* gen. et sp. nov. 106

1. Permineralized fruit, lateral view prior to sectioning, with apex broken. Note widely spaced longitudinal ribs. UF 5665. ×4.
2. Permineralized fruit, lateral view prior to sectioning, with part of pedicel and perianth disk persisting at base, showing elliptical outline and smooth surface. Holotype, USNM 355493. ×4.

3, 4. Same, stereo-pair, basal view, showing circular perianth disk and faint longitudinal ribs. ×4.

5. Same, transverse section, showing thin pericarp, and single locule with numerous ovoid seeds in parenchymatous tissue. RL, ×8.
6. Transverse section of the specimen in fig. 1, showing single large locule with numerous seeds. Etched, RL, ×8.
7. Fracture surface through a permineralized fruit, showing rounded surface of seeds embedded in parenchyma. UF 5673. SEM, ×15.
8. Section of the same specimen, showing the peripheral regions of two neighboring seeds. Note the adjacent parenchyma cells and the finely interwoven cells of the seed coat. RL, ×100.

9–12. *Pollostosperma dictyum* gen. et sp. nov. 105

9. Lateral view showing reticulate surface and rounded margins meeting to form an angle at hilum. USNM 355448. SEM, ×50.
10. Same, face view showing apical dorsal keel. SEM, ×50.
11. Larger specimen, lateral view. Holotype, UF 9830. ×50.
12. Same, enlarged. SEM, ×100.

13–16. *Pruniticarpa cevallosii* gen. et sp. nov. Holotype, UF 9209. 106

13. Endocarp, lateral view, showing longitudinal rib of carpel closure. Transverse line is the plane of section seen in fig. 15. ×1.5.
14. Same, base, showing circular outline, pedicel scar and a single longitudinal rib. PC, ×1.5.
15. Same, transverse section, showing thick wall of endocarp with suture at top of the figure, and single locule with remains of a thin seed coat inside. RL, ×2.
16. Same, enlarged to show cells composing the endocarp and the suture horizontally oriented. RL, acetate peel, ×20.

Explanation of Plate 57

Figure Page

1–3. *Pteronepelys wehrii* gen. et sp. nov. ×5. 106

- 1. Specimen showing wing with straight upper margin and convex lower margin, and elliptical endocarp. OMSI Pb1381.
- 2. Specimen showing three or more sepals arising from the endocarp, right side, and wing with three strong subparallel veins. Holotype, OMSI Pb1018.
- 3. Well-preserved specimen from the Clarno White Cliffs locality, showing acutely pointed distal wing margin, and two style arms protruding from the endocarp. UF 11696.

4–8. *Pulvinisperma minutum* gen. et sp. nov., seed casts. SEM, ×30. 107

- 4. Lateral view, showing rounded base, pointed micropylar projection. Holotype, UF 9740.
- 5. Lateral view. UF 9741.
- 6. Lateral view. UF 9742.
- 7. Face view, showing narrow width, apical keel and hilum. UF 9743.
- 8. Lateral view. UF 9849.

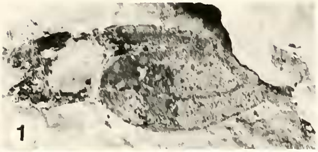
9–12. *Pyrisemen attenuatum* gen. et sp. nov. 107

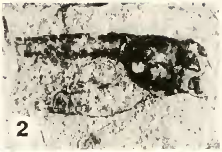
- 9. Chalcedony cast, face view, showing pointed apex and rounded basal truncation. UF 6402. SEM, ×15.
- 10. Chalcedony achene cast, lateral view, tilted back slightly to show circular scar at base. Holotype, UF 6463. SEM, ×15.
- 11, 12. Stereo-pair of the same, achene preserved in translucent silica showing silhouette of the seed cast inside. TL and RL, ×10.

13–19. *Quintacava velosida* gen. et sp. nov. Holotype, USNM 424805. 108

- 13. Lateral view, showing rounded subconical shape. ×4.5.
- 14, 15. Stereo-pair of base, showing the central pedicel scar and the rounded bulges of the five lacunae. ×4.5.
- 16. Transverse section near base, showing five radially arranged slender pyrenes alternating with the lacunae. RL, ×5.
- 17. Detail of wall, transverse section, showing uniseriate locule lining (right side), rows of vertically oriented fibers and scattered circular resin/gum ducts. RL, ×24.
- 18. Same, note lack of lining bordering lacunae (left side). RL, ×24.
- 19. Transverse section showing isodiametric cells of the pericarp. TL, ×45.

20. *Pruniticarpa cevallosii* gen. et sp. nov., detail of cells composing endocarp. Locule and thin seed coat are to the right. Holotype, UF 9209. RL, ×55. 106


1


2


3


4


5


6

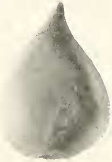

7

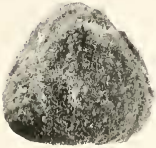

8


9

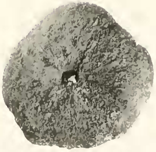

10

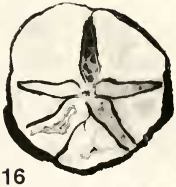

11


12

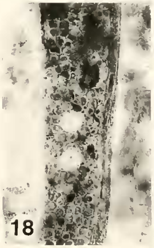

13

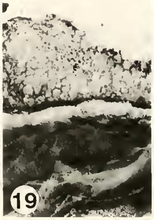

14

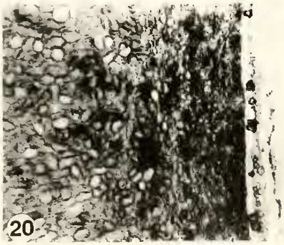

15


16


17


18


19


20


1


2


3


4

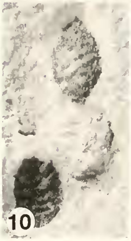

5


6


7


8


9

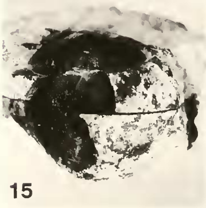

10


11

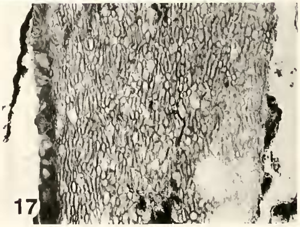

12

13


14


15


16


17

EXPLANATION OF PLATE 58

Figure Page

1–9. *Scalaritheca biseriata* gen. et sp. nov. 109

1. External view of a fruit with part of the wall fractured away revealing a row of elongate, curved seeds. Holotype, UF 5674. ×8.
2. The same, sectioned longitudinally through the row of about even seeds. ×8.
3. Same specimen sectioned longitudinally at right angles to the section in fig. 2, showing median septum, and a row of seven seeds.
4. Specimen fractured longitudinally showing the thick median septum and two rows of about eight seeds. UF 6107. ×10.
5. An isolated seed from one of the fruits. UF 9603. SEM, ×18.
6. Specimen showing the median septum adjoined by a row of intact seeds (right) and the impression of a row of dislodged seeds (left). UF 6281. SEM ×10.
7. Same, light microscopy. PC, ×8.

8, 9. Same, rotated 90°, stereo-pair. ×8.

10–14. *Sambucuspermites rugulosus* gen. et sp. nov. 108

10. Group of three seeds in siltstone. OMSI Pb1716. ×12.
11. Seed cast. UF 6398. ×30.
12. Seed cast, dorsal view, showing ovate outline and rugulate surface sculpture. Holotype, UF 6424. SEM, ×32.
13. Same, ventral view, showing low median ridge leading to the hilum (h), and rugulae. SEM, ×32.
14. Same, lateral view, showing thin profile. SEM, ×30.

15–17. *Sphaerosperma riesii* gen. et sp. nov. Holotype, UF 9746. 110

15. Specimen in siltstone matrix, showing globose morphology, wall partially broken away revealing dark silicified inner tissue. Transverse line is saw mark indicating the plane of section for figs. 16, 17. ×1.5.
16. Transverse section, showing wall of uniform thickness surrounding disrupted inner tissue. RL, × 1.5.
17. Section showing detail of wall, locule to the left. Note lining of rectangular to columnar sclereids and uniform tissue making up remainder of wall. ×40.

EXPLANATION OF PLATE 59

Figure		Page
1–7.	*Scabraecarpium clarnense* gen. et sp. nov.	108
	1. Endocarp, lateral view specimen showing obovate outline and warty surface sculpture. Holotype, USNM 355066. ×1.	
	2. Same, apical view showing circular outline.	
	3. Endocarp, lateral view, showing warty surface sculpture, rounded apex apex and nearly flat base. USNM 354201. ×1.	
	4. Same, apical view, showing lateral compression, elliptical outline. ×1.	
	5. Transverse section of holotype specimen in fig. 1, showing circular outline, thick fruit wall and single circular locule. RL, ×2.	
	6. Transverse section, specimen in figs. 3, 4, showing elliptical outline, single locule and stratification within fruit wall. RL, ×1.5.	
	7. Anatomy of endocarp, transverse section, showing files of rectangular cells and oblique fibrovascular traces. UF 8481. RL, ×15.	
8–17.	*Scaphicarpium radiatum* gen. et sp. nov.	109
	8. Infructescence in matrix with ellipsoidal fruits radiating from central receptacle. Holotype, USNM 312750. ×2.5.	
	9. Chalcedony locule cast removed from infructescence in fig. 8, dorsal view showing pointed apex, rounded base and smooth surface. ×7.5.	
	10, 11. Stereo-pair of the same, lateral view. ×7.5.	
	12. Same, locule cast, apical view showing convex dorsal surface and concave ventral surface of locule cast. ×7.5.	
	13. Transverse section of fruit removed from infructescence in fig. 8, showing crescent shaped locule and ventral infold of the condyle. ×7.5.	
	14. Transverse section of specimen with intact pericarp, showing crescent shaped locule cast. UF 9523. ×12.5.	
	15. Transverse section of specimen with the seed, endocarp and mesocarp tissues intact. USNM 355368. ×10.	
	16. Detail of mesocarp from fig. 14. ×65.	
	17. Isolated locule cast, ventral view showing central circular placental scar. UF 5238. ×7.5.	


1


2


3


4


5


6

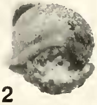

7


8


9


10


11


12


13

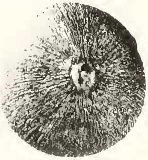

14


15

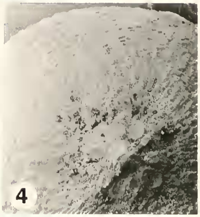

16


17


1

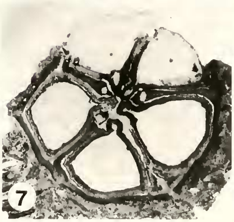

2


3


4


5


6


7

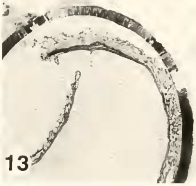

8

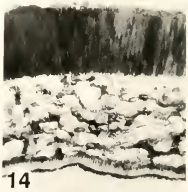

9


10


11


12


13


14

Explanation of Plate 60

Figure Page

1–6. *Striatisperma coronapunctatum* gen. et sp. nov. 111

1. Seed, lateral view, showing longitudinal striations and rounded outline. Holotype, USNM 424694. PC, ×6.4.
2. Same, basal view, showing circular outline and radiating striations. PC, ×6.5.
3. Same, apical view. PC, ×6.5.
4. Apical view of a specimen showing rectangular cells making up the striations and a cycle of about 11 circular scars surrounding the apex. UF 8812. SEM, ×10.
5. Two seeds adjacent in matrix, with a placenta between them. UF 8718. PC, ×5.8.
6. Detail of surface showing one layer of rectangular cells stripped away to reveal another similar surface. USNM 424873. SEM, ×15.5.

7–10. *Sphenosperma baccatum* gen. et sp. nov. Holotype, UF 5666. 110

7. Transverse thin section, showing nearly circular outline of fruit, and five well developed seeds. RL, ×5.
8. Same, enlarged, showing an undeveloped seed (arrow) between two fully developed seeds. RL, ×6.5.
9. Same, showing T-junction of septum with fruit wall, with a seed on each side of the septum. RL, ×20.
10. Closeup of the seed coat, showing inner layer (right) of isodiametric cells, and outer layer of columnar cells. RL, ×50.

11–14. *Stockeycarpa globosa* gen. et sp. nov. Holotype, UF 9747. 111

11. Fruit exposed in matrix, showing spheroidal shape and smooth outer surface. ×5.
12. Same, sectioned transversely, showing circular outline. RL, ×5.
13. Same, enlarged showing parenchymatous layer partially pulled away from the outer layer. RL, ×8.
14. Detail of the wall showing inner thin layer of anticlinally elongate cells, middle layer of parenchyma, and outer layer of anticlinally oriented fibers. RL, ×40.

EXPLANATION OF PLATE 61

Figure Page

1–9. *Tenuisperma ellipticum* gen. et sp. nov. 112

1. Seed, face view, showing rounded base, protruding apex and smooth surface. Holotype, UF 6108. ×5.

2–3. Same, stereo-pair, lateral view, showing thin, wavy profile and characteristic band with a medial groove running from near the apex to the base formed by the margins of the two cotyledons. ×5.

4. Detail from same specimen, lateral view showing folded nature of the lateral band terminating near apex. ca. ×10.

5–6. Stereo-pair, face view. UF 9528. ×5.

7. Same, basal view, showing the marginal band. ×5.

8. Same, face view, showing cell pattern on the surface. ×35.

9. Same, transverse section, locule to the left, showing anticlinally oriented columnar cells of the inner seed coat. ×50.

10–18. *Trigonostela oregonensis* gen. et sp. nov. 112

10. Chalcedony endocarp cast, lateral view, showing pointed apex, elongate outline, and longitudinal grooves between carpels, with some of the wall flaked away exposing smooth locule cast. Holotype, USNM 424671. PC, ×8.5.

11. Chalcedony locule cast with remains of the endocarp adhering apically. UF 6297. PC, ×7.5.

12, 13. Stereo-pair of a permineralized endocarp. USNM 424672. PC, ×8.

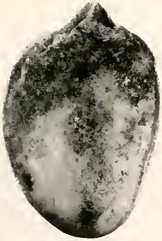
14. Same, rotated 120°, showing median line of septum. PC, ×8.

15. Same specimen as in fig. 10, apical view, showing tricarpellate construction, with one of the locule casts partially exposed (lower right). USNM 424671. PC, ×8.

16. Same as in fig. 11, apical view, ×8.

17. Transverse section showing remains of two of the septa, and large locules. USNM 424674. RL, ×15.

18. Transverse section of permineralized specimen showing collapsed locules completely filled by elongate cells. USNM 435042. RL, ×15.


1


2


3


4


5


6


7


8


9


10

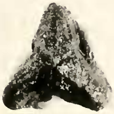

11


12


13


14


15


16


17


18


1


2


3


4

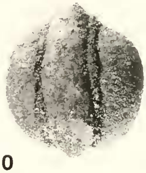

5

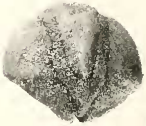

6


7

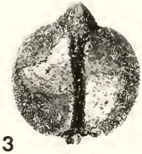

8


9


10


11


12


13


14


15

EXPLANATION OF PLATE 62

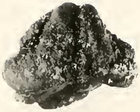
Figure		Page
1–7.	*Tiffneycarpa scleroidea* gen. et sp. nov. Holotype, USNM 355645.	112
1.	Basal view of endocarp with mass of siltstone adhering, lower right. PC, ×3.5.	
2, 3.	Stereo-pair, lateral view showing ellipsoidal outline, longitudinal fibrous grooves and oblique fracture, apex lost. PC, ×3.5.	
4.	Transverse section near base of fruit showing hollow central column and the base of three locules. RL, ×4.	
5.	Transverse section at a higher level, intercepting seven locules. A line of loculicidal dehiscence extends from each locule. Three additional dehiscence lines indicate the position of abortive locules, so that the total number of carpels was ten. Etched, RL, ×6.	
6.	Transverse section near equator, showing central cycle of vascular traces alternating with the locules. Etched, RL, ×6.	
7.	Detail of locule containing remains of seed coat, and showing polygonal cells of the endocarp and dehiscences line. TL, ×17.	
8–15.	*Tripartisemen bonesii* gen. et sp. nov.	113
8–11.	Silicified seed with seed coat stripped away showing casts of internal chambers. Holotype, UF 9288. PC, ×10.	
8.	Basal view showing Y-shaped partition dividing seed into three chambers: two large lateral chambers and a wedge-shaped central chamber, each of these chambers represented by a smooth chalcedony cast.	
9.	Ventral view, showing the hilum at base, lateral chambers and apical protrusion of the central chamber.	
10.	Dorsal view showing full length of the three chambers. Note the facet near the base of the central chamber, and the longitudinal ribs at the junction of the septa with the (now missing) seed coat.	
11.	Apical view, showing rounded dorsal side and V-shaped ventral side.	
12–13.	Another specimen. UF 9296. PC, ×10.	
12.	Basal view, showing hilar scar at the junction of the three chambers.	
13.	Ventral view.	
14.	Transverse section of a seed showing the Y-shaped septa and a portion of adhering seed coat, upper right. UF 9578. RL, ×10.	
15.	Transverse section of a seed with embryo in central chamber. UF 9577. RL, ×10.	

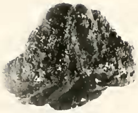
EXPLANATION OF PLATE 63

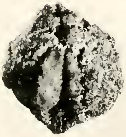
Figure		Page
1–12.	*Triplascapha collinsonae* gen. et sp. nov.	113
	1, 2. Stereo-pair, lateral view, prior to sectioning, showing two locule casts and remains of a disk-like structure near the apex. Holotype, UF 9472. PC, ×7.5.	
	3, 4. Stereo-pair, same, basal view, showing two intact, broadly concave, smooth-surfaced locule casts; another locule cast inferred from symmetry (lower part) is missing. PC, ×7.5.	
	5, 6. Stereo-pair, lateral view, prior to sectioning. USNM 354051. ×7.5.	
	7, 8. Stereo-pair, same, apical view, showing circular outline of disk-like structure, and trigonal symmetry. PC, ×7.5.	
	9. Transverse section of a specimen in matrix, showing two of the three locules. UF 9480. RL, ×5.	
	10. Transverse section of the specimen in figs. 5–8, showing all three locules each with an intact seed. RL, ×7.5.	
	11. Transverse section of the specimen in figs. 1–4. RL, ×7.5.	
	12. Same, enlarged, showing anatomical details including layer of anticlinally elongate columnar cells and outer layer of parenchymatous mesocarp. RL, ×50.	
13–20.	*Triplexivalva rugata* gen. et sp. nov.	114
	13. Fruit, basal view, showing large pedicel scar, three valves and rugulate surface. USNM 424798. PC, ×6.	
	14. Same, apical view, showing coarser rugulae and central scar. PC, ×6.	
	15. Larger, more triangular specimen, basal view. UF 5237. PC, ×4.5.	
	16. Same, lateral view. PC, ×4.5.	
	17. Small specimen, basal view, with two valves shed, upper side of photo, revealing smooth locule cast. Holotype, USNM 424799. ×8.	
	18. Same, apical view, showing coarser rugulae. PC, ×8.	
	19. Same, lateral view. PC, ×7.	
	20. Specimen with two of the valves partially broken away showing thickness of wall. USNM 422396. PC, ×4.3.	


1

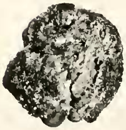

2

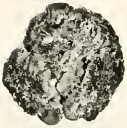

3


4


5

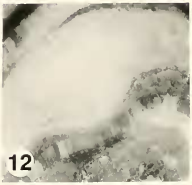

6


7

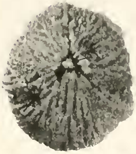

8


10


11

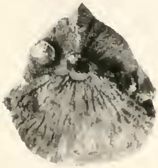



13

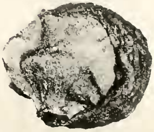

14

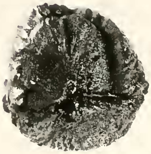

15


16


17


18

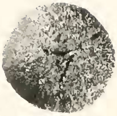

19


20

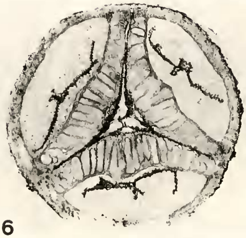

1


2


3


4

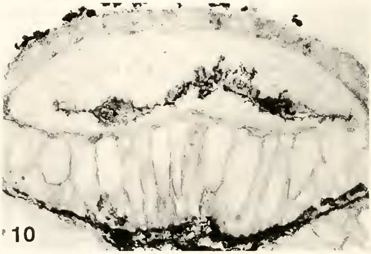

5


6


7


8


9


10


11


12


13


14

EXPLANATION OF PLATE 64

Figure Page

1–10. *Trisepticarpium minutum* gen. et sp. nov. Holotype, USNM 424737. . . . 115

1. Lateral view, showing pyriform outline, rounded apex and narrow, truncate base. PC, ×12.

2–3. Stereo-pair of the same, rotated 120°. Median groove occurs between adjacent carpels. Arrows indicate the levels of sections illustrated in figs. 5–9. PC, ×12.

4. Apical view, showing circular outline and trigonal mark delineating the three carpels.

5. Transverse section showing thin fruit wall and thick septa dilineating three locules with flattened seeds. RL, ×25.

6. Transverse section, showing flattened seeds within the locules. Acetate peel, TL, ×25.

7. Transverse section at a higher level, with a large central triangular space and flattened locules. RL, ×25.

8. Transverse section near the base. RL, ×25.

9. Transverse section near the apex, with one of the locules broken away. Note axile bulges, suggesting subapicial axile placentation. RL, ×25.

10. Transverse section enlarged to show columnar cells of the septum and reticulate seed coat of the seed. Acetate peel, TL, ×65.

11–14. *Truncatisemen sapotoides* gen. et sp. nov. 115

11. Lateral view, showing smooth surface, elliptical outline and oblique truncation. Holotype, UF 6459. PC, ×4.

12, 13. Same, stereo-pair, ventral view, showing narrow width, and a central depression within the elliptical outline of the truncation. PC, ×4.

14. Lateral view of specimen showing thin seed coat partially flaked away, longitudinal crease that may represent groove in embryo or endosperm, raised hilar scar at center of the oblique truncation. USNM 424650. PC, ×5.5.

Explanation of Plate 65

Figure — Page

1–8. *Ulospermum hardingae* gen. et sp. nov. — 115

1. Chalcedony locule cast, lateral view, with some of the endocarp adhering to the attachment region. USNM 414509. PC, ×2.5.
2. Chalcedony locule cast showing concave scar of attachment, micropylar/stylar point and relatively smooth surface with fine punctae. UF 9566. PC, ×2.5.
3. Same, transverse view showing oblong, rounded outline, and complex attachment scar with numerous protruding vacular strands. ×2.5.
4. Specimen in matrix with adhering endocarp, oriented transversely, showing complex attachment scar. Holotype, USNM 355363. ×3.
5. Same specimen in same orientation, partially sectioned to show wall thickness. ×2.5.
6. Same, detail of endocarp wall showing two lacunae or resin ducts. RL, ×25.
7. Endocarp wall showing thin uniseriate locule lining, surrounded by a layer of anticlinally aligned small cells that grade into an outer layer of larger cells. RL, ×40.
8. Acetate peel section of the same. TL, ×50.

9–16. *Wheelera lignicrusta* gen. et sp. nov. UF 9271. — 116

9, 10. Stereo-pair of fruit prior to sectioning, with apical portion of pericarp broken away exposing the locule cast. PC, ×4.

11. Transverse section, showing single locule with thick wall. RL, ×5.

12. Same, more enlarged to show somewhat shriveled seed coat within the locule. Note dark layer of locule lining (endocarp) surrounded by anticlinally oriented cells of the mesocarp. RL, ×6.5.

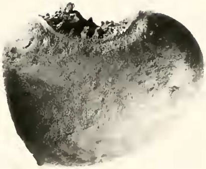
13. Same, basal view showing nearly circular outline. PC, ×4.

14. Same, apical view. PC, ×4.

15. Detail of pericarp showing anticlinally oriented short fibers. RL, ×20.

16. Same, showing columnar cells of the locule lining, many containing rhomboidal crystals (seen in section as white squares). RL, ×70.


1


2


3

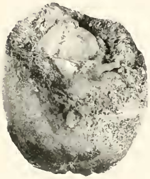

4


5


6


7

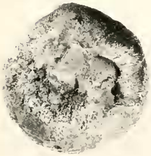

8

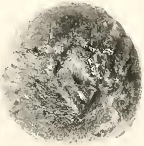

9

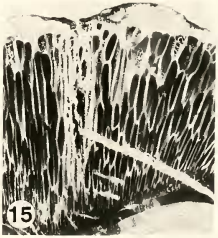

10


11


12


13


14


15


16


1


2


3

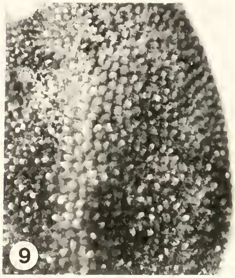

4

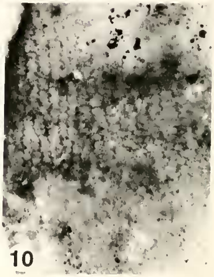

5


6


7

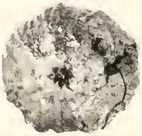

8


9


10


11

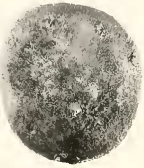

12


13


14


15


16


17


18

EXPLANATION OF PLATE 66

Figure Page

1–10. *Carpolithus bellispermus* Chandler. 116

1. Seed, dorsal view, showing ovate outline and intact asymmetrical hilar region. UF 8544. ×16.
2. Seed, dorsal view, with well-preserved seed coat, broken apically. UCMP 10696. ×16.
3. Same, ventral view. ×16.
4. Complete specimen viewed ventrally with transmitted and reflected light showing silhouette of rounded endosperm cavity with obliquely truncate apex. UF 8545. ×16.
5. Internal mold of seed coat, ventral view, showing low, rounded, median ridge and obliquely truncate hilar region. UF 8554. PC, ×16.
6. Same, basal view, showing rounded dorsal surface, and low, rounded, median ventral ridge. SEM, ×25.
7. Transverse section showing tuburculate seed coat. UF 6607. ×20.
8. Same, detail of of tuburculate cells comprising the seed coat. ×40.
9. Detail from fig. 3, showing tuberculate outer surface of seed coat. ×35.
10. Paradermal view of cells making up the inner layer of seed coat observed through the translucently preserved outer layer of seed coat of seed in fig. 4. UF 8545. ×80.

11–14. *Carpolithus* sp. 1. USNM 355686. PC, ×5. 117

11, 12. Stereo-pair, showing elliptical outline and longitudinal ribs.
13. Basal view, showing stellate central scar and radiating longitudinal ribs.
14. Apical view, showing cleft, left side, and prominent longitudinal ribs.

15, 16. *Carpolithus* sp. 2. USNM 424719. 117

15. Achene, lateral view, showing truncate base, rounded margins and cratered surface. SEM, ×20.
16. Same, tilted to show base with smooth elliptical scar. SEM, ×20.

17, 18. *Carpolithus* sp. 3. USNM 355069. 117

17. Lateral view, showing wide elliptical outline and smooth surface. PC, ×5.
18. Transverse section, showing the thick wall of seed and pair of thick cotyledons. RL, ×5.

EXPLANATION OF PLATE 67

Figure — Page

1–5. *Carpolithus* sp. 4. USNM 424652. — 117

- 1, 2. Stereo-pair, ventral view, showing median longitudinal ridge. PC, ×8.
- 3, 4. Stereo-pair, lateral view, showing smooth surface. PC, ×8.
- 5. Transverse section, showing the seed coat pulling away from the locule at upper left. RL, ×15.

6–8. *Carpolithus* sp. 5. UF 9758. — 117

- 6. Transverse thin section, showing a single locule with a shriveled seed coat. RL, ×20.
- 7. Same, enlarged, showing thick endocarp surrounded by a uniseriate layer of thin-walled rectangular cells. RL, ×50.
- 8. Detail of fruit wall, showing interdigitating cells of the endocarp, the surrounding uniseriate layer of thin-walled rectangular cells, and an outer layer of smaller rectangular cells. RL, ×150.

9–12. *Carpolithus* sp. 6. USNM 424738. — 118

- 9. Fruit in lateral view prior to sectioning. PC, ×7.
- 10. Basal view, showing more or less circular outline, and central attachment scar. PC, ×7.
- 11. Equatorial transverse section, showing thick-walled seed or endocarp with a keel in plane of symmetry and a veruccate outer surface, surrounded by mesocarp composed of large cells. RL, ×10.
- 12. Transverse section at a level 1/3 of the distance from the equator to the base, showing placental attachment area. RL, ×10.

13–16. *Carpolithus* sp. 7. USNM 355637. — 118

- 13, 14. Stereo-pair, apical view, showing smooth to wrinkled surface, roughly circular truncation. PC, ×4.
- 15, 16. Stereo-pair, lateral view, showing the domed apical truncation, rounded sides and base. PC, ×4.


1

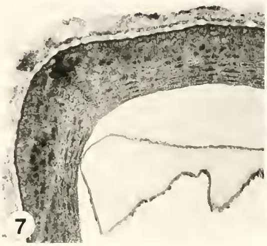

2

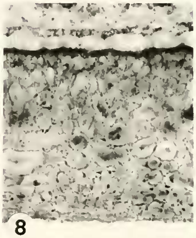

3


4

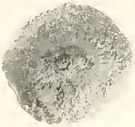

5


6


7

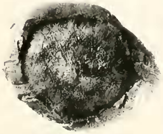

8


9

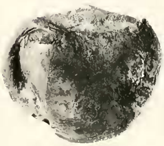

10

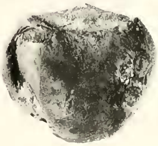

11


12


13


14

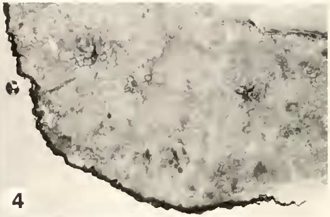

15


16


1


2


3


4


5


6


7


8


9


10


11


12

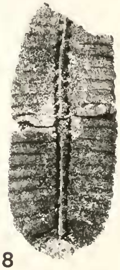

13


14


15


16


17


18


19

EXPLANATION OF PLATE 68

Figure		Page
1–4.	*Carpolithus* sp. 8. USNM 422526.	118
	1. Lateral view, showing truncate base, rounded margins. PC, ×6.5.	
	2. Basal view, showing circular scar. PC, ×6.5.	
	3. Tranverse section showing thick wall, and single locule. RL, ×8.	
	4. Transverse thin section, showing wall made up of more or less isodiametric cells. RL, ×50.	
5–9.	*Carpolithus* sp. 9.	118
	5. Specimen viewed laterally, showing one of the three longitudinal keels, and protruding basal projection. UF 9556. SEM, ×14.	
	6. Same, tilted to show triangular pattern at base. SEM, ×14.	
	7. Specimen viewed basally, showing triangular pattern, central circular area. UF 6457. SEM, ×14.	
	8. Apical view of a specimen in matrix with part of the outer wall intact. UF 9550. SEM, ×14.	
	9. Same as fig. 7, light microscopy. UF 6457. RL, ×14.	
10–14.	*Carpolithus* sp. 10.	119
	10. Ventral view, showing triangular outline and elliptical hilum/funicle. USNM 435102. SEM, ×21.	
	11. Same, oblique lateral view, showing depth of seed. SEM, ×23.	
	12. Similar seed, ventral view, partially broken apically, showing curved embryo cavity within. USNM 435103. SEM, ×24.	
	13. Another specimen, apical view, showing keel (fractured) in line with hilum. USNM 435105. SEM, ×23.	
	14. Same specimen as in fig. 12, lateral view, showing relatively flat ventral margin, convex dorsal margin. SEM, ×20.	
15–19.	*Carpolithus* sp. 11. USNM 424625. PC, ×5.	119
	15, 16. Stereo-pair, ventral view, showing lateral ruminations that are interrupted in the medial area.	
	17, 18. Stereo-pair, dorsal view, showing median keel, and lateral ruminations.	
	19. Lateral view, showing ventrally concave curvature and narrow outline.	

EXPLANATION OF PLATE 69

Figure Page

1–4. *Carpolithus* sp. 12. USNM 326719. 119

1. Chalcedony cast of fruit, lateral view, showing smooth rounded surface, with meridional grooves between the carpels. PC, ×3.
2. Same, basal view, showing five radially arranged carpels. PC, ×3.
3. Same, apical view, showing a median keel on each of the carpels suggesting loculicidal dehiscence. ×3.
4. Same specimen, sectioned transversely, showing radially arranged thin septa, some of which are ruptured, and empty locules. RL, ×5.

5–8. *Carpolithus* sp. 13. UF 9744. 119

5. Lateral view of endocarp with adhering bits of siltstone, showing ovoid shape. ×3.
6. Transverse section showing thick, more or less circular endocarp separated from the outermost thinner exocarp. RL, ×5.
7. Same, enlarged to show endocarp composed of short, anticlinally oriented thin-walled cells. Locule is at top of fig. RL, ×40.
8. Same transverse section showing exocarp composed of densely packed sclereids. RL, ×40.

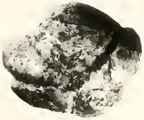
9–12. *Carpolithus* sp. 14. UM 66137. 119

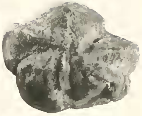
9. Lateral view. ×3.
10. Basal view, showing central attachment scar and circular outline, ×3.
11. Transverse section, showing central group of seeds and surrounding parenchyma tissue, ×3.
12. Same, detail showing three pairs of seeds, one pair fully developed, ×8.

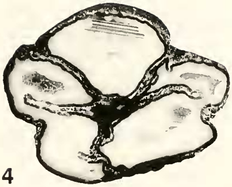
13–16. *Carpolithus* sp. 15. UF 9548. 120

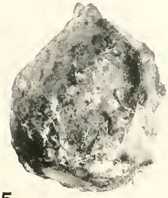
13. Ventral view, showing concave surface and two-lobed morphology. PC, ×8.
14. Dorsal view, showing convex surface and apical and basal clefts. PC, ×8.
15. Lateral view, showing strongly curved outline. PC, ×8.
16. Ventral view, enlarged to show striated pattern of cells on the surface. PC, ×25.


1


2


3

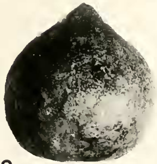

4

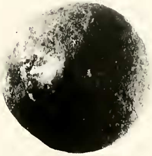

5


6


7


8


9


10


11


12


13


14


15


16


1


2

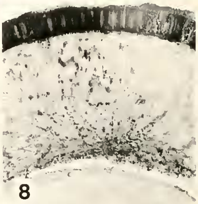

3

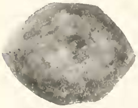

4


5

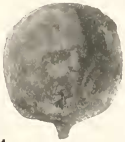

6


7

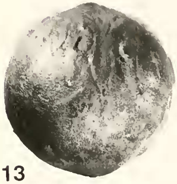

8

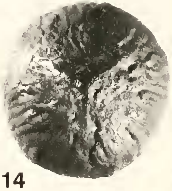

9

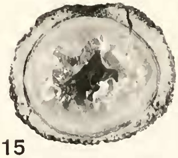

10

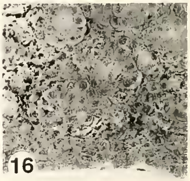

11


12

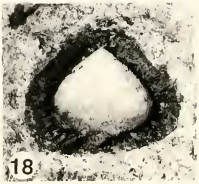

13


14


15


16


17


18

EXPLANATION OF PLATE 70

Figure — Page

1–5. *Carpolithus* sp. 16. 120
  1–2. Stereo-pair of a block of sediment containing numerous seeds preserved as molds of the outer rugulate surface and casts of the inner seed cavity. UF 9794. ×4.
  3. Internal mold of seed coat nested within the carbonaceous external mold of seed coat, viewed laterally. UF 9795. ×10.
  4. Similar view of another specimen. UF 9798. SEM, ×10.
  5. Silicone cast of the specimen in figs. 1, 2, showing rugulate surface pattern of the seeds. SEM, ×10.

6–8. *Carpolithus* sp. 17. UF 9768. 120
  6. Locule cast with some of the pericarp adhering, viewed laterally. Equatorial cuts indicate position of transverse section shown in figs. 7, 8. ×6.
  7. Transverse section, showing thick wall and locule with a single seed. RL, ×10.
  8. Same, showing parenchymatous layer surrounded by a uniseriate layer of anticlinally elongate sclereids. RL, ×25.

9–12. *Carpolithus* sp. 18. UF 6497. 120
  9. Basal view, showing compressed hexagonal outline, with central pedicel, and median keel. ×5.
  10, 11. Stereo-pair, lateral view, showing thick pedicel attachment and rounded apex. ×5.
  12. Transverse section, showing thin fruit wall and empty locule. RL, ×8.

13, 14. *Carpolithus* sp. 19. USNM 422381. PC, ×2.5. 121
  13. Lateral view, showing rounded outline and longitudinal striations.
  14. Apical view, showing triradiate keel.

15, 16. *Carpolithus* sp. 20. UF 9759. 121
  15. Transverse section showing nearly circular locule lined with quartz crystals, and irregular thickness of the eroded pericarp. RL, ×5.
  16. Same, showing detail of isodiametric sclereids composing the pericarp. RL, ×60.

17. Five-parted flower. ×1.3 121

18. *Carpolithus* sp. 21. USNM 422525. ×4.3. 121

NOTES ADDED IN PROOF

1. Recent geologic mapping in the type area of the Clarno Formation has provided new information and an alternative interpretation of the local stratigraphic succession (Bestland et al., 1994, and written communication). The porphyritic unit immediately northeast of the Nut Beds, previously identified as an andesitic plug (p. 9), is now considered to be a dacite dome, composed of plagioclase-hornblende porphyritic dacite. Bestland et al. conclude that this dome was already a weathering topographic feature at the time of Nut Beds deposition because bake zones and alterations of the surrounding sediments are not evident, and because reworked clasts of the dacite occur in conglomerates within the Nut Beds. Whereas C. B. Hanson (1973) interpreted the Nut Beds to be separated by an unconformity from the mudflow deposits of Hancock Canyon, Bestland et al. consider these units to be approximately coeval.

Bestland, E. A., Retallack, G., and Fremd, T.

1994. *Geology and age assessment of late Eocene fossil localities in the Clarno Unit, John Day Fossil Beds National Monument, central Oregon.* Geological Society of America, Rocky Mountain Section, Abstracts with Programs, vol. 5, p. 4.

2. A samara of *Cedrelospermum* was recently recovered from Messel, Germany, confirming the presence of this genus in the Middle Eocene of central Europe. In conformity with other European representatives of the genus, it has a terminal stigmatic cleft and lacks the small secondary wing typically found in North American species (Manchester, 1987b). The specimen, Me 7274, is in the paleobotanical collection of the Senckenberg Museum, Frankfurt and was examined through the courtesy of Prof. Friedemann Schaarschmidt.

3. Fruits of *Cruciptera* have now been described and illustrated in detail on the basis of specimens with excellent cuticular preservation from the Middle Eocene of Messel, Germany. *Cruciptera schaarschmidtii* samaras are about half the size of *C. simsonii* samaras, but the two species are difficult to distinguish morphologically. Epifluorescence microscopy of the Messel specimens reveals that *Cruciptera* possessed peltate glands, another character attesting to its affinity with the Juglandaceae (Manchester et al., 1994).

Manchester, S. R., Collinson, M. E. and Goth, K.

1994. *Fruits of the Juglandaceae from the Eocene of Messel, Germany, and implications for early Tertiary phytogeographic exchange between Europe and western North America.* International Journal of Plant Sciences, vol. 155 (in press).

4. In addition to vitaceous seeds, the grape family is represented in the Nut Beds by anatomically preserved wood. Based on a thorough survey of available extant vitaceous woods, Wheeler and La Pasha (1984) recognize two distinct taxa in the Nut Beds, both of which are assigned to a new extinct genus, *Vitaceoxylon* Wheeler et LaPasha. Although the fossil species are vines with anatomical characters diagnostic of Vitaceae, they do not conform to any one extant genus of the family. This new information from woods raises the intriguing possibility that seeds morphologically identical to those of certain modern genera might have occurred on vines that were anatomically distinct from modern genera.

Wheeler, E. A. and LaPasha, C. A.

1994. *Woods of the Vitaceae—fossil and modern.* Review of Palaeobotany and Palynology, vol. 80, pp. 175–207.

INDEX

Note: Page numbers are in light face type; the page numbers for principal discussions or descriptions are in *italic* type. Plate numbers are in **bold face** type.